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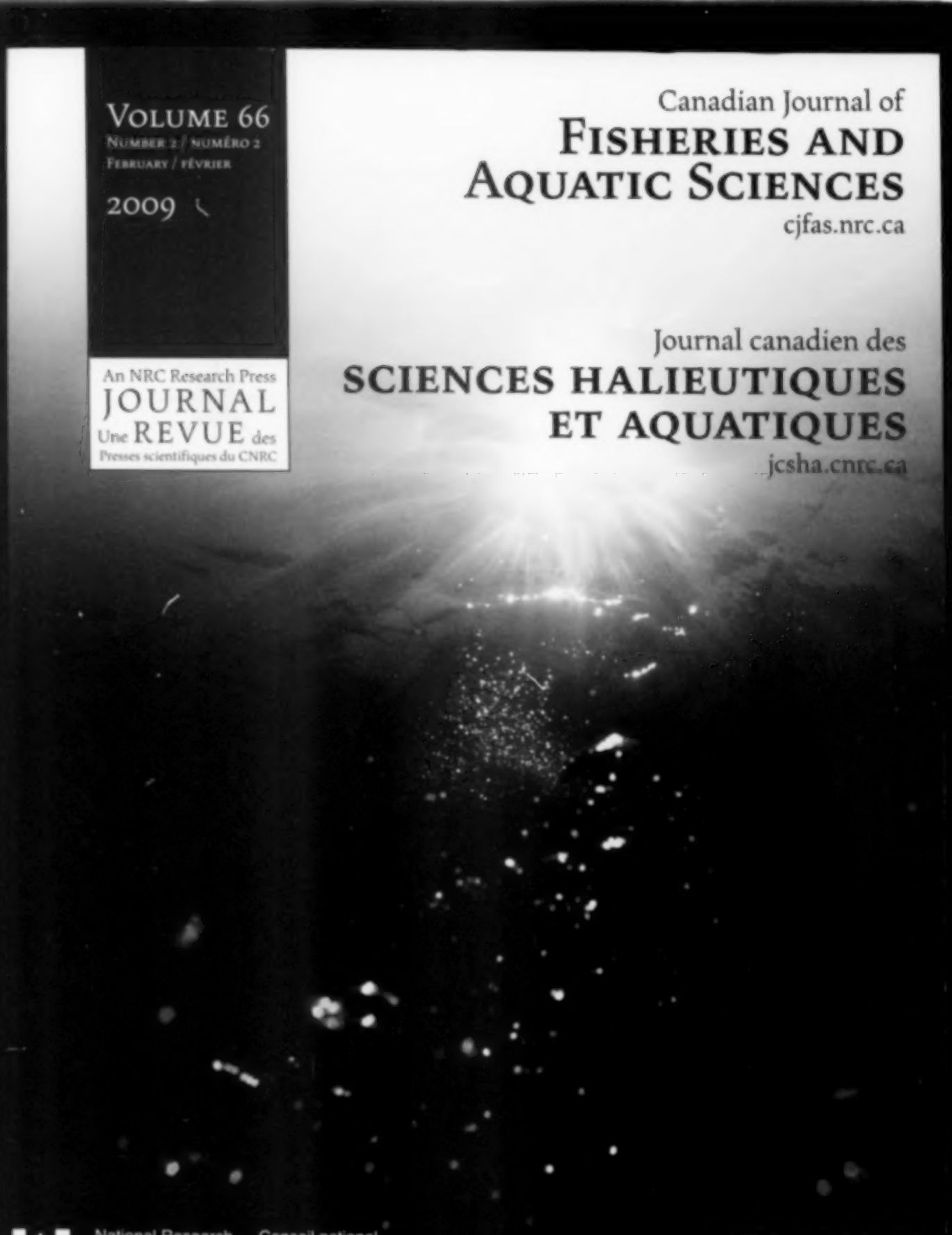

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Gene flow increases temporal stability of Chinook salmon (*Oncorhynchus tshawytscha*) populations in the Upper Fraser River, British Columbia, Canada

Ryan P. Walter, Tutku Aykanat, David W. Kelly, J. Mark Shrimpton, and Daniel D. Heath

Abstract: Temporal instability in population genetic structure has significant implications for management and conservation decisions. Here, we evaluate temporal stability in five populations of Chinook salmon (*Oncorhynchus tshawytscha*) from the Upper Fraser River, British Columbia, Canada, based on estimates of temporal allelic variance and effective population size (N_e) at 11 microsatellite loci. Significant temporal variation in allele frequencies was found within individual populations sampled at 5- to 12-year intervals. Removal of migrant fish or correcting for migrants resulted in higher allelic variance or reduced N_e. Populations with higher levels of temporally consistent gene flow show reduced temporal allelic variance (i.e., reduced genetic drift) and higher N_e. This study is an important empirical example of the effect of gene flow on genetic stability and N_e. In salmonids, low straying levels may have evolved to favor local adaptation; however, we show that even such low levels of gene flow can elevate effective population sizes and preserve genetic variability. This study highlights the importance of considering gene flow acting to temporally stabilize populations, particularly small ones, and should migration be interrupted, N_e levels may decline with no obvious change in census population sizes.

Résumé : L'instabilité temporelle de la structure génétique de la population a des conséquences importantes pour les décisions reliées à la gestion et la conservation. Nous évaluons ici la stabilité temporelle de cinq populations de saumons chinook (*Oncorhynchus tshawytscha*) du Fraser supérieur, Colombie-Britannique, Canada, d'après des estimations de la variance allélique temporelle et de la taille effective de la population (N_e) à 11 locus microsatellites. Il existe une variation temporelle significative de la fréquence des allèles dans les populations individuelles échantillonnées à des intervalles de 5–12 ans. Le retrait des poissons migrateurs ou l'addition d'une correction pour tenir compte des migrateurs entraînent une variance allélique plus élevée ou une N_e réduite. Les populations qui possèdent des niveaux plus élevés de flux génique stable dans le temps ont une variance allélique temporelle réduite (donc une dérive génétique réduite) et une N_e plus élevée. Notre étude constitue un exemple empirique important de l'effet du flux génique sur la stabilité génétique et sur N_e. Chez les salmonidés, les degrés faibles d'errance ont peut-être évolué pour améliorer l'adaptation locale; nous montrons, cependant, que même de tels niveaux faibles de flux génique peuvent faire augmenter la taille des populations effectives et préserver la variabilité génétique. Notre travail souligne l'importance de tenir compte du flux génique qui peut entraîner la stabilisation temporelle des populations, particulièrement de celles de petite taille; si la migration était interrompue, les valeurs de N_e pourraient décliner sans changement évident dans la taille des populations recensées.

[Traduit par la Rédaction]

Introduction

Analyses of population genetic structure using microsatellite markers have widespread application in evolutionary and conservation biology. Those applications include the identification of populations of specific conservation concern, such as those severely bottlenecked or otherwise displaying reduced genetic diversity. However, the supposition of little or no recent genetic change (i.e., genetic stability) can be misleading as allele frequencies may fluctuate temporally as a consequence of variation in factors such as effective population size (N_e), species range and dispersal, and life history. For example, random drift based genetic change may confound conservation-based analyses testing for changes in genetic composition resulting from anthropogenic or environmental effects on population processes (Heath et al. 2002). Temporal genetic samples are available for a number of aquatic species because of their high abundance in nature and the availability of archived material. This is especially true of commercially important fish species, including cod

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(Ruzzante et al. 1997; Poulsen et al. 2006), sea basses (Rhodes et al. 2004), and various salmonids (Østergaard et al. 2003; Palm et al. 2003; Jensen et al. 2005). Among salmonids, there is no consistent pattern of genetic stability, as some studies have reported stable genetic structure and composition (Tessier and Bernatchez 1999; Hansen et al. 2002; Heath et al. 2002), and others have reported genetic instability (Østergaard et al. 2003; Palm et al. 2003; Jensen et al. 2005). As more studies are published with estimates of temporal genetic change, the potential for identifying the factors affecting temporal stability will likely increase.

Previous work in salmonids has demonstrated that, theoretically, significant variation in spatial and temporal genetic structure may result from interactions between drift and local adaptation (Elo 1993; Adkinson 1995). Although variation at gene loci is driven by selection, mutation, drift, and gene flow, small populations will encounter elevated drift effects and may appear to be less stable over time due to stochastic effects alone. This elevated variance may be tempered by intermittent gene flow serving to inflate local N_e (Slatkin 1985). For example, gene flow between life history stages within a single river has been shown to have a stabilizing effect on N_e (Araki et al. 2007). Alternatively, episodic gene flow among genetically divergent populations may artificially inflate allele frequency variance, increasing apparent genetic instability and leading to low estimates of N_e. With this in mind, relatively small populations that experience gene flow are ideal models in which to assess factors that affect temporal genetic stability, as genetic drift is likely to be high and the effect of gene flow is likely to be profound.

Pacific salmonids are particularly useful species in which to examine the relationship between gene flow and genetic stability as high levels of natal philopatry result in low rates of straying (Altukhov et al. 2000). The resulting limited gene flow among even geographically close populations often leads to differentiation via genetic drift and local adaptation (Taylor 1991; Quinn 1993; Heath et al. 2006). Indeed, a number of studies using microsatellite loci show particularly high levels of genetic structure in salmonid populations (e.g., Taylor 1995; Nielsen et al. 1997).

We use an historical microsatellite marker data set (1978–1998) from Shrimpton and Heath (2003) to test novel hypotheses concerning the temporal stability of allele frequencies in five populations of Chinook salmon (*Oncorhynchus tshawytscha*) in the Upper Fraser River, British Columbia, Canada. Chinook salmon were sampled at approximately 10-year intervals from the late 1970s to the late 1990s, and those samples proved useful for the determination of N_e (Shrimpton and Heath 2003). Here, we first quantify temporal changes in genetic structure and allele frequency distribution to test the hypothesis that populations are temporally stable. We then examine the relationship between migration and temporal stability to test the hypothesis that gene flow through time reduces temporal allelic variance and raises N_e, thereby lending to increased population viability in the long term.

Materials and methods

Study areas

The five study populations for which microsatellite genotype data from Shrimpton and Heath (2003) were available are shown in Fig. 1. The Nechako River (N), Stuart River (S), Willow River (W), Bowron River (B), and Dome Creek (D) populations were chosen based on the availability of archived scale samples, close geographical proximity, and well-documented historical information. Within the last 30 years, census population sizes have either increased from moderate (Bowron) or very low numbers (Willow), remained small (Dome), remained relatively stable over time (Nechako), or shown considerable annual variation (Stuart; Shrimpton and Heath 2003). For each river, scale samples of adult spawners were collected at two or three dates over a 20-year period (1978–1998). Sample size for each population ranged from 29 to 60 individuals, except Bowron 1998, which consisted of 18 individuals. Allele frequency data were calculated for dinucleotide repeat markers (Ots1, Ots3, Ots4, Omy207, Omy325, Oneu3, Ssa85, Ssa197, Sfo8) and tetranucleotide repeat markers (Ots104, Ots107). Individuals with genotypes missing at two or more loci and those with rare alleles (<0.01, study-wide across all time periods) were removed from the data set prior to analyses.

Statistical analysis

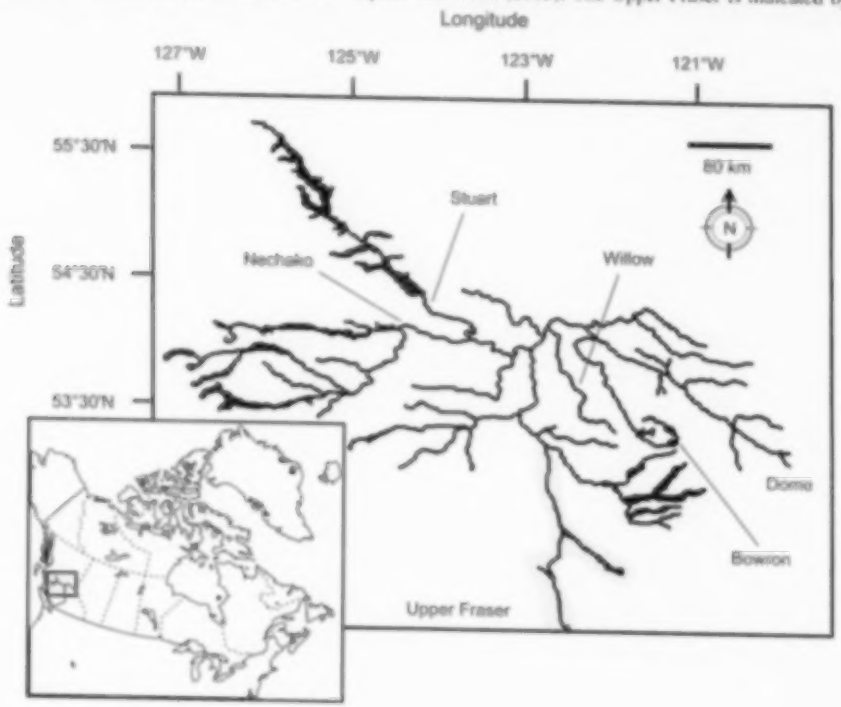
The 11 microsatellite loci used here had high levels of variation in the Chinook salmon populations examined, and nine tests out of 154 showed significant deviation from Hardy–Weinberg equilibrium, but without a consistent pattern. To test for differences in allele frequency distribution among sampling years and populations, we performed pairwise exact tests using TFPGA 1.3 (Miller 1997; 1000 dememorization steps, 20 000 permutations; Raymond and Rousset 1995). To quantify genetic divergence among populations and sampling years, we calculated pairwise F_{ST} (Weir and Cockerham 1984) and estimated significance with 10 000 permutations using MSA software (Dieringer and Schlötterer 2003). We applied Bonferroni correction to maintain an experiment-wide α level of 0.05 for all pairwise comparisons. Principal coordinates analysis (PCoA, covariance-standardized) was performed on the pairwise matrix of F_{ST} values in GENALEX 6.1 (Peakall and Smouse 2006) to show relationships among samples.

To partition allele frequency variance among populations, among sampling years within populations, and among individuals, we performed a hierarchical analysis of molecular variance (AMOVA; Excoffier et al. 1992) using ARLEQUIN software (Schneider et al. 2000). Significance values of the variance components were obtained using 10 000 permutations.

To quantify the degree of temporal allelic variation within each population, we estimated the standardized allele variance ($\hat{F}$; Waples 1989) and effective population size (N_e; Waples 1989) using N_e ESTIMATOR (Peel et al. 2004). Estimates of N_e were corrected for overlapping generations by multiplying N_e estimates by mean generation times (Shrimpton and Heath 2003). Both estimates were calculated for each pairwise temporal comparison within populations.

To determine the influence of migration on temporal stability we identified first-generation migrants based on population exclusion methods in GENECLASS 2.0 (Piry et al. 2004) using the Bayesian method (Rannala and Mountain 1997) and the likelihood ratio of L_{home} to L_{max} (Paetkau et

Fig. 1. Map of the Upper Fraser River watershed (British Columbia, Canada) showing the locations of the five rivers where spawning Chinook salmon samples were collected. Map redrawn from Shrimpton and Heath (2003). The Upper Fraser is indicated by shading.



al. 2004). Monte-Carlo resampling was performed with 10 000 simulated individuals at an assignment threshold P value of 0.05. We compared D_{LR} values and F_{ST} estimates among populations to determine whether detection of migrants is possible (Paetkau et al. 2004). We then recalculated allelic variance ($\hat{F}$) and moments-based N_e in all populations with the identified migrants removed. To determine whether a reduction in sample size resulted in a change in $\hat{F}$ following removal of migrants, we randomly removed individuals (equal numbers as the identified migrants) from each temporal sample in 10 replicates and then recalculated $\hat{F}$ (Appendix A, Fig. A1).

To further illustrate the influence of migration on temporal stability, we also calculated N_e via two methods using the maximum-likelihood approach of Wang and Whitlock (2003) in the software MNE 2.0. N_e is inversely proportional to drift and, hence, temporal allelic variance. To determine the effect of migrant fish on N_e, we first estimated N_e assuming "closed" populations on the original data set and then reran the analysis following removal of the migrants identified by GENECLASS. Next we estimated N_e allowing migration (e.g., "open" model) between focal populations (T_1, T_2, and T_3 for Nechako, Stuart, Bowron, and Dome; T_1 and T_2 for Willow) and a source population. Source populations consisted of pooled genotypes from all samples and time periods except the focal population, a technique that is suggested to be robust (Wang and Whitlock 2003). Generation times of 1 were used for temporal samples separated by 5 years, 2 for 8, 10, and 12 years, and 4 for 20 years. N_e estimates were corrected for overlapping generations using the mean generation times as in Shrimpton and Heath (2003). We then compared estimates of all three N_e estimates and their respective N_c–N_e ratios to see whether trends were consistent across methods.

To determine directionality of gene flow among populations, we obtained estimates of migration rate (m) using BAYESASS 1.2 software (Wilson and Rannala 2003). Runs were performed allowing migration among samples in three temporally relevant groupings: (*i*) N-78, S-80, B-80, and W-80; (*ii*) N-88, S-88, B-88, and D-86; and (*iii*) N-98, S-98, B-98, and D-96. Estimates of m were taken from averages of three replicate runs of 5×10^7 iterations, with 3×10^7 burn-in runs and five subsequent replicate runs of 3×10^7 to identify convergence among runs.

Results

Exact tests revealed significant differentiation in population genetic structure for all pairwise comparisons ($P < 0.001$) following Bonferroni correction. All pairwise F_{ST} estimates were significant following Bonferroni correction with only four exceptions, only one of which was a spatial comparison (Table 1). The MDS plot of genetic differentiation among populations illustrates the magnitude of temporal variation for some populations compared with others (Fig. 2). For example, the proximity of data points for temporal samples from the Nechako and Stuart populations compared with those of the Dome or Bowron populations. The AMOVA showed significant genetic differentiation

among sampling years, within populations (1.63%, $P < 0.001$), and among populations (1.21%, $P < 0.005$).

Of the 590 individuals in the data set, 76, or roughly 13%, were identified as migrants based on GENECLASS analysis, with Dome Creek harbouring the highest number of identified migrants and the Stuart showing the fewest (Appendix A, Table A1). D_{LR} and F_{ST} measurements from pairwise population comparisons showed that sufficient discriminatory power was available to detect migrants (Table 1; Appendix A, Table A1). The subsequent exclusion of migrant individuals from our samples amounted to removal of an average of five individuals per site study wide, resulting in the retention of approximately 87% of all individuals across all samples (Appendix A, Table A1). Following removal of migrants, the average sample size was 37 individuals per site. As predicted, increases in allelic variance were noted for all populations for all temporal samples following removal of migrants (Fig. 3*a*). Moments-based estimates of N_e showed similar results in that N_e decreased in all populations except the early comparison from the Bowron (Fig. 3*b*). Recalculation of $\bar{F}$ following random removal of individuals from each temporal sample (numbers equal to the number of migrants identified) did not yield changes in $\bar{F}$ comparable with those following migrant removal, thus the effect of removing migrants is not a result of the reduction in sample size (Fig. A1).

Calculations of N_e using the Wang and Whitlock (2003) methods showed consistently higher N_e when migrants were included in the samples (Fig. 4*a*). As N_e estimates are less sensitive to sample sizes, the use of N_e and its subsequent decrease following migrant removal exemplifies the stabilizing effect of the migrants across the study system, independent of sample size effects. Furthermore, the estimates of N_e using the "open" model were comparable with those using the "closed" model with migrants removed (Figs. 4*a*, 4*b*). Comparison of N_e–N_c ratios shows that this pattern is evident independent of census population size (Fig. 4*b*).

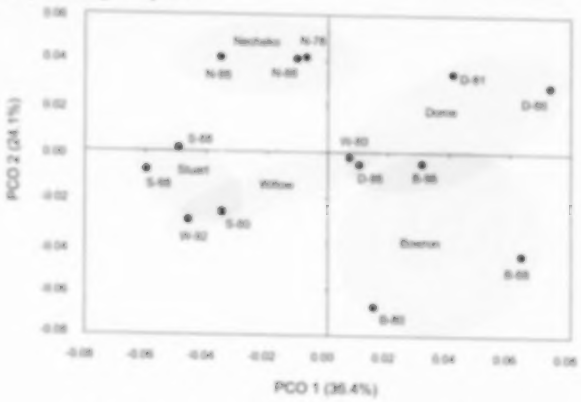
Estimation of migrations rates from BAYESASS showed mean migration rates across all sampling periods of 0.032 for Nechako, 0.099 for Bowron, and 0.064 for Stuart. Migration rates estimates for the Dome 1986–1988 suggested a possible local optimum trap in BAYESASS at 0.33 migration rate, most likely due to a violation of the assumption of <1/3 migrants (Wilson and Rannala 2003; Austin et al. 2004; Hansen et al. 2007). Work by both Faubet et al. (2007) and Palstra et al. (2007) demonstrates the limitations of BAYESASS for estimating recent migration rates; therefore the following migration estimates should be interpreted with caution. BAYESASS indicated asymmetrical gene flow (i.e., non-overlap of confidence intervals) from the Nechako into the Stuart in the temporal sampling period 1978–1988 (Table 2). However, all other migration rates appeared to be bidirectional because of overlap in confidence intervals, despite some suggestion of asymmetrical migration again from Nechako into the Stuart for the 1998 samples (Table 2). For the populations and temporal periods in which BAYESASS was able to reliably estimate migration, both Dome (0.0106) and Nechako (1978, 0.0133; 1998, 0.0229) showed that the lowest incoming rates were smaller. Across all time periods, the Bowron received the most migrants, and within the 1986–1988 sampling period, the Dome appeared to be a

Table 1. Pairwise F_{ST} for spatiotemporal comparisons of five populations of Chinook salmon (*Oncorhynchus tshawytscha*) from the Upper Fraser River.

	Nechako			Dome			Willow		Bowron			Stuart		
	N-78 (49)	N-88 (60)	N-98 (48)	D-86 (29)	D-91 (58)	D-96 (59)	W-88 (27)	W-92 (30)	B-80 (36)	B-88 (34)	B-98 (18)	S-80 (55)	S-88 (44)	S-98 (43)
N-78														
N-88	0.006													
N-98	0.009	0.014												
D-86	0.040	0.038	0.059											
D-91	0.025	0.025	0.034	0.017										
D-96	0.042	0.029	0.047	0.032	0.031									
W-80	0.018	0.021	0.024	0.040	0.038	0.036								
W-92	0.051	0.044	0.037	0.075	0.057	0.032	0.032							
B-80	0.048	0.052	0.058	0.056	0.051	0.041	0.032	0.040						
B-88	0.050	0.052	0.069	0.040	0.039	0.051	0.034	0.076	0.020					
B-98	0.032	0.033	0.043	0.041	**0.023**	0.046	**0.028**	0.053	0.044	0.025				
S-80	0.027	0.026	0.026	0.065	0.046	0.033	0.025	0.021	0.026	0.046	0.028			
S-88	0.029	0.024	0.024	0.069	0.046	0.042	0.040	0.030	0.047	0.066	0.045	**0.014**		
S-98	0.033	0.031	0.032	0.087	0.058	0.046	0.049	0.040	0.048	0.071	0.054	0.022	0.024	

Note: Sample sizes are given in parentheses after sample name; all P values for F_{ST} estimates are significant at $P < 0.01$, except bold values, which are significant at $P < 0.05$, and underlined values, which are not significant at $P > 0.05$.

Fig. 2. Multidimensional scaling plot of pairwise F_{ST} among populations and sampling dates. Shaded ovals indicate spatial relationships among samples.



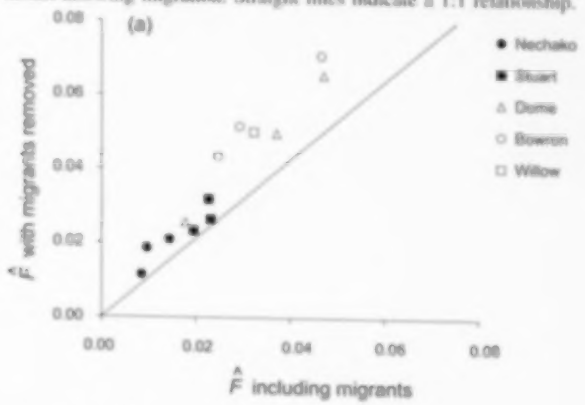
source of migrants for both the Nechako and Bowron populations (Table 2).

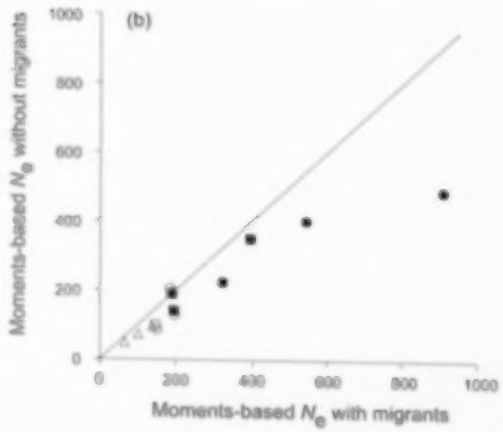
Discussion

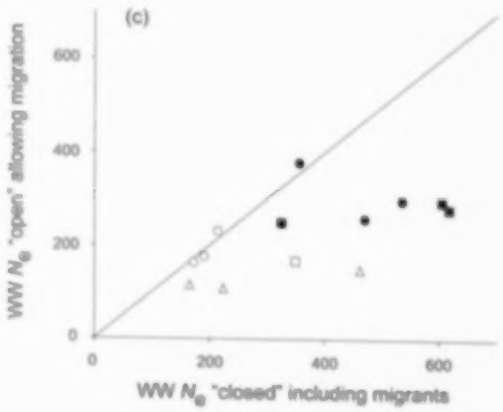
Temporal instability in allele frequency distribution was found for all populations of Chinook salmon sampled from tributaries to the Upper Fraser River, with the overall magnitude of temporal within-population variation exceeding that of among-population variation. The level of stability of some populations (Nechako, Stuart) is consistently higher than that of others (Willow, Dome, Bowron). The temporal predictability of genetic structure among populations varied from nearly wholly consistent to essentially random, which may explain some of the inconsistencies among previous temporal studies of genetic structure in salmonids. Earlier work has reported both stable (Tessier and Bernatchez 1999; Hansen et al. 2002; Heath et al. 2002) and unstable (Laikre et al. 2002; Østergaard et al. 2003; Jensen et al. 2005) population genetic composition and structure in salmonids. Our results indicate that genetic stability clearly varies among populations of Chinook salmon, even within the restricted geographical range of the Upper Fraser River.

Three possibilities may account for the variability in population genetic stability among the geographically close Chinook salmon populations of the Upper Fraser River. First, within-season variation in the genetic composition of the spawning run coupled with changes in the sampling time could drive temporal instability. Fillatre et al. (2003) showed that comparisons of early- and late-run sockeye salmon (*Oncorhynchus nerka*) accounted for twice the genetic variation observed among years within the same river. However, we know of no records of multiple spawning run structure for Chinook in our study populations but cannot exclude the possibility of within-run temporal variation, as samples were not collected for specific periods within the annual yearly spawning runs. A second source of variation in temporal instability may stem from differential survival or reproductive success among populations. This point is typically well illustrated by comparing N_e with N_c. Although the decoupling of N_e and N_c was shown for these populations by Shrimpton and Heath (2003) and is also observed

Fig. 3. Effects of migration on (*a*) time-standardized allelic variance ($\hat{F}$), (*b*) translation of $\hat{F}$ estimates to moments-based effective population size (N_e), and (*c*) comparison of Wang and Whitlock (WW, 2003) "closed" estimates including migrants to WW "open" model allowing migration. Straight lines indicate a 1:1 relationship.

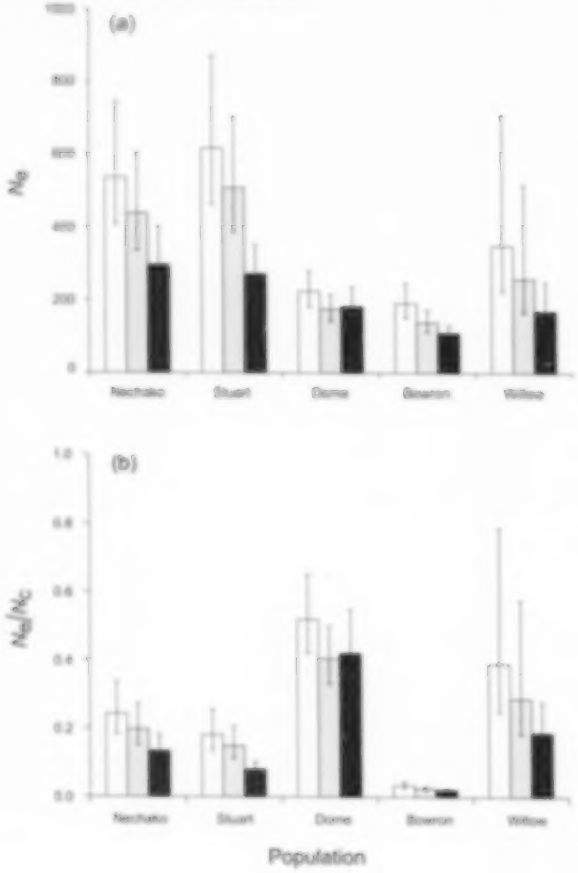






in other salmonids (Araki et al. 2007; Fraser et al. 2007*b*), our estimates of N_e show the persistence of these patterns, despite any buffering effects that gene flow appears to confer. Although this decoupling may suggest that differential

Fig. 4. (*a*) Study-wide comparative estimates of N_e using Wang and Whitlock (WW, 2003) "closed" models both with (open bars) and without (shaded bars) migrants and WW "open" model allowing migration (solid bars). (*b*) Study-wide ratio of effective population size to census population size (N_e–N_c) estimates for N_e estimated assuming no migration and after correction for migration. Error bars represent 95% confidence limits.



survival and reproduction appears independent of gene flow, the consistent declines in N_e for each population following migrant removal or correction further demonstrate that gene flow is the third possibility driving temporal variation in these populations.

Generally, gene flow is expected to be stabilizing if the rate is constant in magnitude, time, and source (Wang and Whitlock 2003). Our analyses provide empirical evidence that variation in gene flow is likely driving the differences in temporal genetic stability among our sampled populations. Although we conclude that gene flow appears to confer stability for some populations, the relationship between temporal stability, gene flow, and neutral genetic differentiation is perhaps more complex as the effects of gene flow on genetic stability clearly depend not only on the source, but also on the genetic stability of the source population itself.

Philopatry in salmon may have evolved to match locally adapted fish with sites exhibiting similarities in habitat or spawning areas (e.g., Stuart and Nechako), suggesting that genetic stability of a recipient population likely depends on the drift-based variance of the source population. The Nechako and Stuart populations exhibited the greatest temporal stability, but the Stuart shows that migration rates from outside are nearly 10-fold higher than in the Nechako. The source of migrants for the Stuart is consistently the Nechako over the study period, itself a temporally stable system. Such patterns of gene flow are likely the result of straying among the geographically close Upper Fraser River Chinook salmon populations, as individuals may find it more difficult to distinguish between proximal natal and non-natal sites (Hendry et al. 2004). This dispersal or straying may not reflect individual "choice" (Hendry et al. 2004) as abiotic factors such as environmental perturbation possibly affect straying rates and patterns (e.g., controlled water discharge in the Nechako River may influence straying into the adjacent Stuart River). Furthermore, both habitat degradation and population declines have been noted for these populations (Shrimpton and Heath 2003), which likely impedes assessment of natural or original connectivity patterns (Palstra et al. 2007).

Recent work in salmonids has used patterns of asymmetrical gene flow from large into small populations as evidence for density-dependent dispersal (Fraser et al. 2004; Hansen et al. 2007). This pattern is not observed for our populations; however, directionality of gene flow has been shown to be primarily determined by the temporal scale over which migration was being estimated (Palstra et al. 2007). As we are restricted to estimating gene flow indirectly from point samples between rivers at different times, it is likely that we have not sampled all source populations and our estimates of specific directional migration rates between populations should be interpreted with caution. The migration rates estimated in BAYESASS further illustrate the complexity of the relationship between gene flow and stability as high migration estimates for Bowron 1978 do not translate into higher N_e estimates. This trend is also illustrated by the slight increase in N_e "open" estimates for the Bowron following removal of migrants using both moments-based and Wang and Whitlock's methods. Nonetheless, the effect of correcting for migration on our estimates of $\bar{F}$ and N_e consistently demonstrates the temporally stabilizing potential of gene flow.

A number of studies show gene flow induced genetic stability in other species, perhaps hinting at the generality of this effect. Dispersal (and subsequent gene flow) has been credited for the high temporal genetic stability of coyote populations despite aggressive removal efforts (Williams et al. 2003). Studies in insects have also linked temporal stability to consistent gene flow (Loxdale and Brookes 1990; Bourguet et al. 2000). For species exhibiting metapopulation-type structuring, such as cod (*Gadus morhua*), high migration rates buffer against bottlenecks through inflating N_e, as evidenced by drastic reductions in census sizes but no corresponding changes in N_e (Ruzzante et al. 1997; Poulsen et al. 2006).

This study provides a valuable assessment of Wang and Whitlock's (2003) "open" model for estimating N_e. This model simulates migration between potential source populations and the focal populations at given time periods,

Table 2. Estimates of migration rates among populations and sampling dates using BAYESASS 1.3.

	Into site:			
Source	N-78	W-80	B-80	S-80
N-78	**0.98667** (0.95996, 0.99936)	0.00498 (0.00002, 0.02667)	0.00571 (0.00004, 0.02531)	0.12467 (0.07421, 0.17297)
W-80	0.00320 (0.00001, 0.01523)	**0.97692** (0.92000, 0.99918)	0.09765 (0.00309, 0.19019)	0.00404 (0.00003, 0.01744)
B-80	0.00333 (0.00001, 0.01653)	0.01026 (0.00002, 0.05605)	**0.88204** (0.79293, 0.98085)	0.00582 (0.00005, 0.02283)
S-80	0.00680 (0.00002, 0.02814)	0.00783 (0.00002, 0.03767)	0.01460 (0.00010, 0.05931)	**0.86547** (0.81647, 0.91653)
m	0.01333	0.02308	0.11796	0.13453
	Into site:			
Source	N-88	D-86	B-88	S-88
N-88	**0.94075** (0.89629, 0.97518)	0.00495 (0.00001, 0.02205)	0.00811 (0.00006, 0.03655)	0.01772 (0.00007, 0.06096)
D-86	0.04569 (0.01864, 0.08321)	**0.67707** (0.66702, 0.71099)	0.11796 (0.05783, 0.22797)	0.00561 (0.00002, 0.02226)
B-88	0.00393 (0.00003, 0.01681)	0.31200 (0.26099, 0.32890)	**0.86736** (0.75720, 0.92552)	0.00841 (0.00003, 0.03710)
S-88	0.00963 (0.00006, 0.03567)	0.00456 (0.00001, 0.02138)	0.00658 (0.00005, 0.03191)	**0.96827** (0.91673, 0.99855)
m	0.05925	0.32151	0.13264	0.03173
	Into site:			
Source	N-98	D-96	B-98	S-98
N-98	**0.97704** (0.93524, 0.99892)	0.00261 (0.00001, 0.01369)	0.02060 (0.00008, 0.07173)	0.01729 (0.00007, 0.05531)
D-96	0.00588 (0.00003, 0.02642)	**0.98977** (0.96658, 0.99943)	0.01231 (0.00006, 0.05270)	0.00529 (0.00001, 0.02513)
B-98	0.00987 (0.00005, 0.03472)	0.00290 (0.00001, 0.01494)	**0.95681** (0.88818, 0.99761)	0.00399 (0.00001, 0.01835)
S-98	0.00721 (0.00002, 0.03490)	0.00472 (0.00003, 0.02106)	0.01027 (0.00004, 0.04566)	**0.97344** (0.93224, 0.99858)
m	0.02296	0.01023	0.04319	0.02656

Note: Bold values along the diagonal are the proportion of fish that were assigned to the site of capture and are thus non-migrant fish. Populations are designated by site codes (N, Nechako; W, Willow; B, Bowron; S, Stuart; D, Dome) and years (last two digits). Numbers in parentheses represent the 95% confidence limits. *m*, total migration rate into each population.

thereby N_e estimates using the "open" model should resemble those of the "closed" model following migrant removal. For Atlantic salmon, Fraser et al. (2007*a*) identified N_e "open" estimates that more closely reflected biological reality than higher N_e "closed" estimates in populations that were known to have experienced bottlenecks. Fraser et al. (2007*a*) and Palstra and Ruzzante (2008) further suggest that N_e "open" estimates may be generally biased downwards and N_e "closed" estimates biased upwards. Palstra and Ruzzante (2008) observed upward biases of N_e under N_e "closed" conditions in 94% of their salmonid estimates, signifying that relatively continuous gene flow reduces drift. In this study, the congruence of the N_e "open" estimates to those of the N_e "closed" with migrants removed emphasizes this point that N_e is augmented in Chinook salmon populations and that these populations are not as isolated as previously believed.

The effect of gene flow on genetic stability has implications for the management and ecology of Chinook salmon. First, the implicit assumption that straying in Pacific salmon is rare (and of little ecological relevance for long-term population viability) should be re-evaluated. As is well known, populations with low N_e must be accorded high conservation priority; however, this study shows that even populations with moderately high N_e may be unexpectedly at risk if migrant source populations are impacted. The results of this study thus emphasize the importance of nearby source populations, particularly those that are genetically stable, as they affect local population stability and help to maintain connectivity and long-term population viability. Hence, the definition of management and conservation units should consider temporal stability (and thus N_e) as an important population parameter as it reflects both within-population factors and among-population gene flow (Fraser et al. 2007*a*).

The results of this study are consistent with the hypothesis that populations experiencing regular gene flow may be buffered from temporal genetic variation, resulting in elevated estimates of N_e. From a management perspective, these findings emphasize the value of temporal genetic screening of populations for defining genetic relationships among populations and highlight the importance of gene flow in stabilizing both small and larger populations. As isolation increases genetic instability, isolated populations should be of high management priority. Furthermore, source populations within this system are also of high priority as they contribute to the genetic diversity of receiving populations. Given the range of temporal stability among our study populations, it is clear that no assumptions can be made concerning temporal genetic stability among even geographically close populations of a single species, much less across species.

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Appendix A

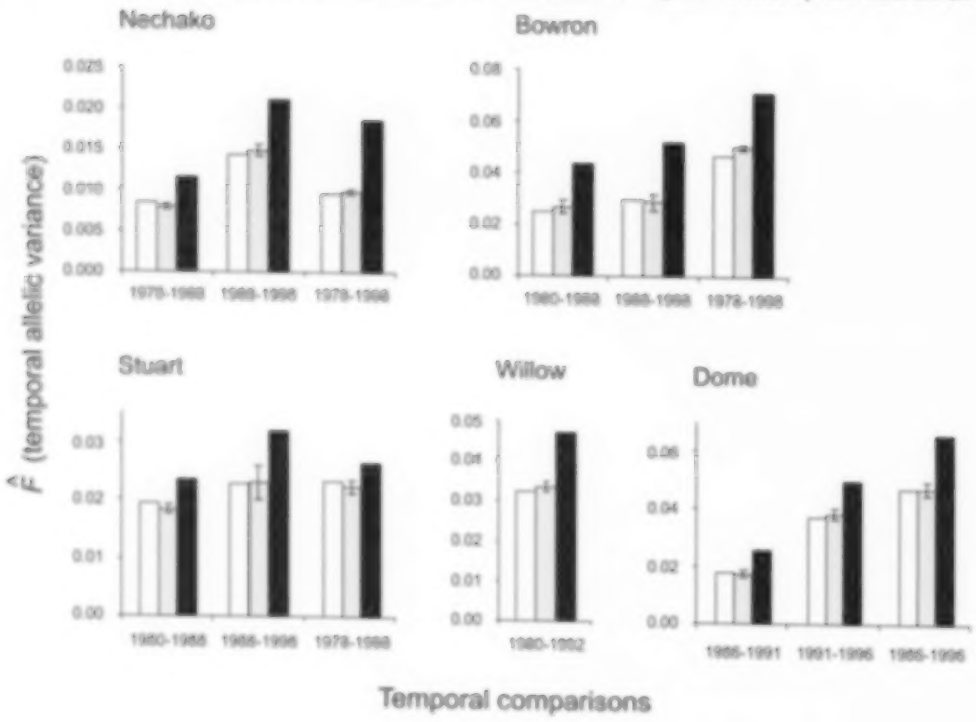
Table A1 and Fig. A1 follow.

Table A1. Number of genotyped fish following removal of first-generation (F_0) migrants identified in each population by GENECLASS.

Population	n	F_0 migrants	% migrants	Mean $D_{A,R}$	n without migrants
N-78	49	5	0.10	2.1	44
N-88	60	3	0.05	2.5	57
N-98	48	8	0.17	3.9	40
D-86	29	5	0.17	4.5	24
D-91	58	6	0.10	4.3	52
D-96	59	11	0.19	4.8	48
W-80	27	7	0.26	2.7	20
W-92	30	6	0.20	2.9	24
B-80	36	7	0.19	2.7	29
B-88	34	5	0.15	3.2	29
B-98	18	3	0.17	4.9	15
S-80	55	2	0.04	2.4	53
S-88	44	2	0.05	4.2	42
S-98	43	6	0.14	3.9	37

Note: Population names follow as listed in the text; n, total number of genotyped fish per population; mean $D_{A,R}$ measures genetic distance between focal population and all others.

Fig. A1. Comparison of $\hat{F}$ estimates with migrants (open bars), removal of random individuals in equal proportion to detected migrants (shaded bars; 10 replicates, error bars represent standard deviation, SD), and removal of migrants detected by GENECLASS 2.0 (solid bars).



The impact of double-crested cormorant (*Phalacrocorax auritus*) predation on anadromous alewife (*Alosa pseudoharengus*) in south-central Connecticut, USA

Christopher M. Dalton, David Ellis, and David M. Post

Abstract: The decline of anadromous alewife (*Alosa pseudoharengus*) threatens an important recreational and commercial fishery. While the cause of this decline is uncertain, predators could be trapping alewives at low abundance by preying on them during spawning migrations. Here we investigate the impact of predation by double-crested cormorants (*Phalacrocorax auritus*) on spawning adult alewives in south-central Connecticut, USA. We use a bioenergetic model together with estimates of cormorant diets and cormorant and alewife population sizes to estimate the consumption of alewives by cormorants both in Bride Lake, Connecticut, and regionally. We find that cormorants are important predators of spawning adult alewives at Bride Lake but do not have a notable impact on alewife mortality or population size. We also find that cormorants have little effect on alewife populations across south-central Connecticut because few alewives are consumed away from Bride Lake. We conclude that cormorants are important predators for anadromous alewives, but do not pose an immediate threat to the recovery of regional alewife stocks.

Résumé : Le déclin de gaspareau anadrome (*Alosa pseudoharengus*) menace une importante pêche sportive et commerciale. Bien que la cause du déclin soit incertaine, les prédateurs pourraient s'emparer des gaspareaux dans les conditions de basse densité en les capturant durant leur migration de fraie. Nous examinons ici la prédation par les cormorans à aigrettes (*Phalacrocorax auritus*) sur les gaspareaux adultes en fraie dans le centre-sud du Connecticut, É.-U. Un modèle bioénergétique combiné à des estimations du régime alimentaire des cormorans et des densités des populations de cormorans et de gaspareaux nous a servi à estimer la consommation de gaspareaux par les cormorans à la fois dans le lac Bride, Connecticut, et dans la région avoisinante. Les cormorans sont d'importants prédateurs de gaspareaux adultes pendant la fraie au lac Bride, mais ils n'ont que peu d'effet marqué sur la mortalité ou la taille de la population de gaspareaux. Les cormorans ont aussi peu d'effet sur les populations de gaspareaux dans tout le centre-sud du Connecticut, parce que peu de gaspareaux y sont consommés sauf au lac Bride. En conclusion, les cormorans sont d'importants prédateurs des gaspareaux anadromes, mais ils ne représentent pas une menace immédiate pour la récupération des stocks régionaux de gaspareaux.

[Traduit par la Rédaction]

Introduction

Anadromous alewife (*Alosa pseudoharengus*) are of notable ecological, economic, and historical importance in eastern North America. They impact freshwater ecosystems by importing marine-derived nutrients (Durbin et al. 1979; Garman and Macko 1998; MacAvoy et al. 2000) and structuring prey communities through predation (Post et al. 2008). The inshore fishery for anadromous alewives dates to precolonial times, and the offshore fishery, still a large source of bait for Atlantic cod (*Gadus morhua*) and American lobster (*Homarus americanus*) fishermen, once landed nearly 25 000 mt annually (Munroe 2002).

Probably because of intense fishing pressure, alewives have declined throughout their native range since the 1960s (Munroe 2002). Several states have outlawed taking anadromous alewives, others are considering similar restrictions, and the US federal government has listed anadromous alewives as a species of concern across their range. Alewife stocks have continued to decline even as resource managers spend millions to restore anadromous fish spawning habitat. Managers suspect that bycatch from the Atlantic herring (*Clupea harengus*) fishery or predation by inshore predators is keeping alewife stocks at low abundance (Savoy and Crecco 1995).

Striped bass (*Morone saxatilis*) and double-crested cormorants (*Phalacrocorax auritus*, henceforth referred to as cormorants) are abundant inshore piscivores that could be preventing alewife recovery (Savoy and Crecco 1995). Striped bass and cormorant populations have increased dramatically in the past 20 years, and both species are more abundant now than ever in recent history (Wires et al. 2001; Hartman 2003). Hartman (2003) estimated that striped

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bass in the Hudson River could consume all of the young-of-the-year river herring (alewife and the closely related blueback herring, *Alosa aestivalis*) produced annually in that watershed, suggesting alewife population decline could be caused by increasingly abundant natural predators. Cormorants are also prodigious predators of fish and, where abundant, may impact alewife populations. Numerous studies have shown that cormorants can impact fish populations by altering population dynamics (Burnett et al. 2002; Rudstam et al. 2004), consuming a large proportion of the known population size (Derby and Lovvorn 1997), or by adding substantial incremental mortality to other known sources (Hebert and Morrison 2003; French McCay and Rowe 2004).

Blackwell et al. (1995, 1997) found that anadromous fish, including alewives, comprised a major but highly variable portion of the cormorants' diet in coastal Maine. We expect that based on their opportunistic foraging strategy (Hatch and Weseloh 1999), cormorants will feed heavily on alewives where spawning runs predictably concentrate thousands of fish in small bodies of water. The extent of such predation remains to be quantified.

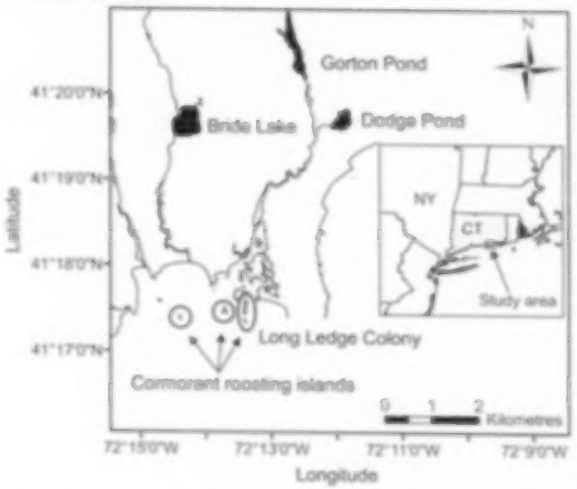
Here, we use a bioenergetic model to estimate the consumption of anadromous alewives by cormorants. The energetic model uses literature estimates of the daily per-cormorant energy intake and direct observation of cormorant population size, diet composition, and prey energy density. We focus our study on Bride Lake, in southern Connecticut, USA, one of the largest remaining alewife runs in Connecticut and host to large flocks of feeding cormorants during the alewife spawning season. Historical and current studies at Bride Lake provide detailed data on the lake's alewife population before and after the recent increase in local cormorant abundance (Kissil 1974; Davis 2004; Post et al. 2008). We use this data in conjunction with cormorant consumption estimates to obtain a high-resolution estimate of the magnitude and impact of cormorant predation on alewives at this lake. We then consider the implications of our result for the sustainability of regional alewife populations.

Materials and methods

Study site

Bride Lake is an 18.2 ha, 10.7 m deep (maximum depth) lake located in East Lyme, Connecticut (Fig. 1; Kissil 1974). There is no public access to Bride Lake because it is surrounded by two correctional facilities and a water treatment plant. The alewife run at Bride Lake is one of the largest remaining in Connecticut, and anadromous alewives obtain access to the lake by Bride Brook, a 3.5 km stream that empties into Long Island Sound at Rocky Neck State Park, Niantic, Connecticut. Daily counts of in-migrating alewives, obtained from the Connecticut Department of Environmental Protection, were made by hand in 2003 and 2004 and by electronic fish counter (Smith-Root, SR-1601) in 2005 and 2006. The fish counter was calibrated against hand counts in 2005. Hand counts were performed using a weir in Bride Lake, upstream of the fish counter, to collect in-migrating alewives. Every 24 h, alewives were picked from the weir by hand net, counted, and then moved into Bride Lake. The weir remained in place throughout in-migration, preventing

Fig. 1. Map showing the study area in Connecticut (inset: location in northeastern USA), including the focal alewife (*Alosa pseudoharengus*) run at Bride Lake, as well as nearby runs at Dodge Pond and Gorton Pond. The three roosting islands for double-crested cormorants (*Phalacrocorax auritus*) feeding at Bride Lake (including the Long Ledge breeding colony) are illustrated in the lower left portion of the map.



spawned-out alewives from leaving Bride Lake until in-migration was complete. The end of in-migration was determined based on historical run dates and daily in-run counts. Several days separated the end of in-migration and the beginning of out-migration. We will refer to the 24 h count of alewives entering Bride Lake as the daily escapement.

The annual alewife mortality in Bride Lake was determined by subtracting the count of alewives leaving Bride Lake from total annual escapement. The count of alewives leaving Bride Lake was obtained from the Smith-Root counter after the weir was removed. Because of concern that unusually high flow might endanger out-migrating alewives (a local and USA federal species of concern), we have no similar estimate of mortality in 2006.

We studied cormorants both at Bride Lake and at several nearby islands in Long Island Sound (Fig. 1). These islands are unvegetated, rocky outcroppings less than 4.0 km from Bride Lake. One of these islands, Long Ledge, serves as a breeding colony for 155–170 pairs of cormorants, while all other islands are used as roosts by nonbreeding cormorants.

Cormorant population estimates

We separately estimated the number of cormorants feeding at Bride Lake and the number of cormorants that potentially could feed at Bride Lake. Estimates of the number of cormorants feeding at Bride Lake were made in both 2005 and 2006 by shore-based observers using binoculars and a spotting scope. In 2005, we performed counts at least once a week between 8 April and 1 May, and in 2006 we performed these counts at least once a week between 5 March and 22 May and at least twice a week between 22 March and 7 May. Counts were performed continuously for several hours. Between 2 h after sunrise and 2 h before sunset, the

count of cormorants on Bride Lake never varied by more than 10 birds. We also surveyed cormorant abundance at two nearby alewife spawning sites (Dodge Pond and Gorton Pond) on each Bride Lake count date. These counts were conducted at the beginning and end of each Bride Lake count and frequently once in the middle of the count as well.

The number of cormorants within foraging range of Bride Lake (henceforth referred to as the local cormorant population) was assessed in 2006 by counting the number of cormorants roosting within 20 km of Bride Lake (studies on the Great Lakes, e.g., Neuman et al. 1997) show that most cormorant foraging occurs within this distance of breeding colonies). These counts included breeding birds on Long Ledge, as well as migrant cormorants roosting on other islands. These birds represented all cormorants feeding in bodies of water near or on the Connecticut shoreline between the Niantic and Connecticut rivers.

Daily cormorant movements were assessed by visual observation. Throughout the spawning season, cormorants were observed leaving roosting islands at dawn and returning at dusk. Because of the proximity of Bride Lake and Long Ledge, cormorants could be observed throughout the flight between the two sites at both dawn and dusk. We never observed a cormorant leave Bride Lake and fly to any roosting site not included in our observations.

Cormorant diets

We estimated the diet of the local cormorant population based on otoliths recovered from cormorant pellets collected at roosts. The identification and measurement of otoliths from cormorant pellets is a method biased by otolith wear and unpredictable retention (Harris and Wanless 1993; Blackwell et al. 1995; Leopold et al. 1998). Nonetheless, we chose to use this method because it is minimally invasive and less prone to spatial and temporal sampling bias per unit effort than other methods, such as stomach dissection or flushing (Harris and Wanless 1993; Votier et al. 2003, reviewed in Wires et al. 2001).

Cormorant pellets were collected from West Brother Island on 9 April (n = 28), 27 April (n = 38), and 7 May 2006 (n = 21). We were unable to find cormorant pellets at other roosting sites in the study area. We chose these three dates to represent the cormorant diet before (9 April), during (27 April), and after (7 May) the peak of alewife abundance in Bride Lake. We collected each pellet in a separate ziplock bag and preserved all pellets at –20 °C within 4 h of collection. For analysis, we dissolved each pellet in 1.0 mol·L^{-1} NaOH for 24 h and removed all of the otoliths from each pellet under a dissecting microscope. We paired as many otoliths as possible from each pellet according to the specific identity, measured size, and whether the otolith was from the right or left side of the fish. We identified each otolith or pair of otoliths to the lowest possible taxon using several guides to otoliths of Atlantic fishes (Broudeur 1979; Harkonen 1986; Campana 2004) and a reference collection of otoliths from 27 species of freshwater, estuarine, and marine fish that we considered potential food sources for cormorants.

For analysis, we regarded either a pair of otoliths or one unpaired otolith as representative of a single fish in the cormorant diet. We measured the total length of each otolith or otolith pair using an optical micrometer. We defined total otolith length as the straight-line distance between the furthest extents of the otolith along its anterior–posterior axis. We estimated the total length (TL) of the consumed fish using taxon-specific otolith length – TL regressions, which we calculated from measurements of reference specimens and published data (Appendix A, Table A1). We then estimated the weight (FW, in g) of each consumed fish using TL–FW regressions from our reference collection and published sources (Appendix A, Table A1). We did not calculate FW for unknown otoliths (<5% of all collected otoliths) and non-fish food items (two unidentified shrimp). For the local cormorant population's diet, we estimated the proportion by weight and frequency of occurrence of each fish taxon for each of our three sampling dates.

To account for the effect of digestive wear on fragile alewife otoliths, we used a linear scalar to correct the average estimated alewife length in the cormorant diet upwards to match that of alewives found entering Bride Lake. We did not perform this correction on other diet items, the otoliths of which are less prone to digestive erosion.

In both 2005 and 2006, we sampled the fish community of Bride Lake using purse seines, beach seines, gill nets, and hook and line. Personnel from Connecticut Department of Environmental Protection monitored the movement of fish in and out of the lake on a daily basis. All of the fish species found in or moving into Bride Lake taken together (excluding alewives) accounted for less than one percent of the diet of cormorants roosting nearby. This result strongly suggests that while cormorants may consume a few freshwater fish at Bride Lake, the vast majority of their diet there is alewife.

Bioenergetics model

We estimated the consumption of alewives both by cormorants at Bride Lake (2005 and 2006) and by the local population of cormorants (2006 only). Our consumption estimates are based on the daily energy intake of a single cormorant, daily estimates of cormorant population size, the empirically determined energy density of prey items, and the proportion of the cormorants' diet composed of alewife.

We estimated the daily energy intake of a single cormorant using a model for daily energy expenditure, or field metabolic rate (FMR), of seabirds (Ellis and Gabrielsen 2002) and a digestive efficiency factor from Brugger (1993). We multiplied this energy intake by daily estimates of cormorant population size at Bride Lake and Long Ledge, using linear interpolation to estimate population between actual counts. This total daily energy intake (kJ) was divided by prey energy density (kJ·g^{-1}) to calculate total daily fish consumption (g, wet mass). Total alewife consumption was then estimated by multiplying fish consumption by the cormorant diet proportion composed of alewives.

We created maximum and minimum estimates for each model input to produce the widest possible range of consumption estimates. Each estimate of alewife consumption was recalculated using all minimum values and all maximum values for model inputs (Table 1). (For more detail on our energetics modeling approach, see Appendix B.)

Table 1. Parameter estimates and range of variation in parameter estimates (minimum–maximum values) used in bioenergetics models.

Input	Midpoint used	Min. and max. values
Cormorant body mass (g)	2050[a]	1861[b]–2442[b]
FMR (kJ·cormorant^{-1})[c]	2390[d]	1581[e]–3817[d]
Count	Direct counts and interpolation	±10%[f]
Digestive efficiency	0.779[g]	0.75–0.79[g]
Alewife energy density (kJ·g^{-1})	5.86	5.71–6.01[a]
Alewife body mass (g)	152	147–158[a]

[a]Glahn and Brugger 1995.
[b]Kury 1969.
[c]Field metabolic rate.
[d]Ellis and Gabrielsen 2002.
[e]Gremillet et al. 2003.
[f]Brugger 1993.
[g]± standard error.

Results

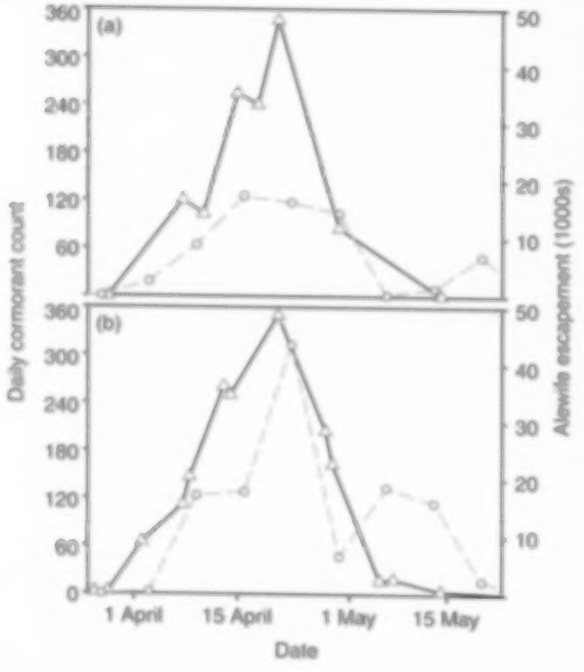
Cormorant and alewife populations

The number of cormorants feeding at Bride Lake was similar in 2005 and 2006 (Fig. 2). In both years, cormorants began feeding at the lake around 1 April, were most abundant (about 350 birds) around 22 April, and were largely gone by 10 May. Daily counts averaged 5% higher in 2006 than in 2005. The number of cormorants roosting on islands near Bride Lake (2006 only; not illustrated) largely paralleled the trend at the lake itself, but peaked later, at 600 cormorants, on 29 April.

Cormorants that fed at Bride Lake during the alewife spawning season spent most of the available daylight on the lake. Their abundance there was consistent from midmorning until early evening. Flocks typically foraged in three feeding bouts: morning, midday, and early evening. Each feeding bout lasted between 1 and 2 h. Between bouts, cormorants rested on the lake surface or in trees overhanging the lake. Most birds departed the lake in flocks immediately after the third foraging bout, at the end of the day. All flocks were observed flying directly from Bride Lake to the studied roosting sites in Long Island Sound. At dawn, flocks of some cormorants, though not all at the roosting site, were observed flying directly to Bride Lake from Long Ledge. Cormorant abundance at other nearby alewife runs never approached that at Bride Lake, with no more than 10 birds on Dodge Lake or Gorton Pond at any time.

Total annual alewife escapement into Bride Lake was 116 851, 81 350, 68 761, and 129 114 in 2003, 2004, 2005 and 2006, respectively (mean across all years = 99 019). Escapement was nearly twice as high in 2006 as in 2005, with much of that additional escapement occurring during 7–10 May. No similar late peak in escapement occurred in 2005. In 2005, and for most of 2006, cormorant abundance at Bride Lake closely tracked daily alewife escapement (Fig. 2). In 2006, however, there was no late peak in cormorant abundance to match the substantial movement of alewives into Bride Lake from 7 to 10 May. In 2005, the overall mortality rate for adult alewives in Bride Lake was 62% (42 888 fish).

Fig. 2. Comparison of alewife (*Alosa pseudoharengus*) escapement and double-crested cormorant (*Phalacrocorax auritus*) abundance at Bride Lake in 2005 (*a*) and 2006 (*b*). Alewife counts (circles, broken line) represent the total number of alewives entering Bride Lake in the previous 7 days. Cormorant counts (triangles, solid line) represent actual full-day cormorant counts made at Bride Lake on each demarked date.



Cormorant diet

In 2006, we assessed the diet of cormorants roosting on islands within foraging range of Bride Lake (the local cormorant diet). Before the peak in alewife abundance at Bride Lake, alewives made up a small proportion of the local cormorant diet (7% by weight, frequency = 0.25). During the

Fig. 3. The estimated diet of cormorants (*Phalacrocorax auritus*) roosting near Bride Lake. The estimated diet is the proportion (by weight) of fish eaten by cormorants roosting near Bride Lake and is presented for alewife (*Alosa pseudoharengus*; black), white perch (*Morone americana*; gray), marine fish (open), and other freshwater fish (hatched).

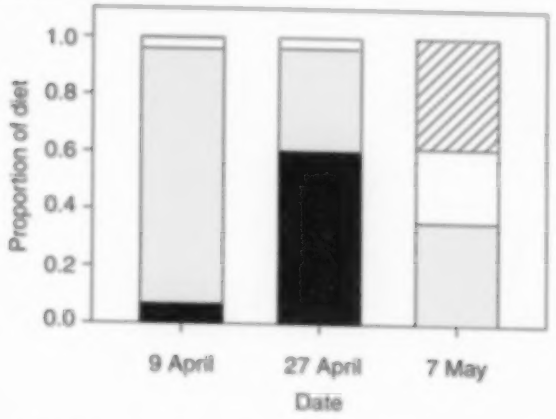
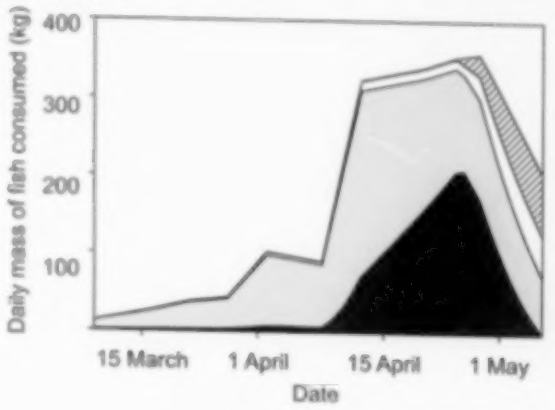


Fig. 4. The daily estimated fish consumption by cormorants (*Phalacrocorax auritus*) roosting near Bride Lake. Consumption is estimated for alewife (*Alosa pseudoharengus*; black), white perch (*Morone americana*; gray), marine fish (open), and other freshwater fish (hatched).



height of the alewife run, alewives made up more than half (60% by weight, frequency = 0.67) of the local cormorant diet. By 7 May, however, pellets collected from cormorant roosts contained no evidence of alewives (Figs. 3, 4).

For the entire sampling period, white perch (*Morone americana*) were the most abundant fish by weight in the local cormorant diet (Figs. 3 and 4). White perch were most prevalent in early April (89% by weight, frequency = 0.63), but were less abundant at each subsequent sampling date. Other freshwater fish species were never more than a minor portion of the diet of these cormorants. Saltmarsh fish species (*Fundulus* spp. and *Menidia menidia*) and other marine fish were increasingly abundant in cormorant diets through the spring sampling period, but never accounted for more than 25% of fish consumed (by weight; Fig. 3).

Our intensive fish sampling efforts in Bride Lake found alewives, bluegill (*Lepomis macrochirus*), yellow perch (*Perca flavescens*), largemouth bass (*Micropterus salmoides*), white sucker (*Catostomus commersonii*), and banded killifish (*Fundulus diaphanus*) in the lake. All of these species together (excepting alewives) accounted for less than one percent of the fish eaten by cormorants roosting near Bride Lake in 2006. We found no evidence of white perch in Bride Lake, but they are common in the Connecticut River, a nearby river where flocks of cormorants from this population feed.

Cormorant consumption and alewife mortality estimates

We estimate that cormorants at Bride Lake consumed 20 687 alewives in 2005 (range 11 417–39 923) and 23 705 alewives in 2006 (13 083–45 747). At Bride Lake, cormorant consumption of alewives increased 15% from 2005 to 2006; however, the proportion of alewives entering Bride Lake that were consumed by cormorants decreased from 30% in 2005 to 18% in 2006. In 2005, we estimate that 48% of overall alewife mortality was caused by cormorants.

In 2006, we estimate that all cormorants roosting within foraging range of Bride Lake (the local cormorant population) consumed 22 954 (range 10 797–49 968) alewives. This estimate was 3% lower than our estimate for cormorants at Bride Lake alone in the same year. This result strongly suggests that cormorants roosting near Bride Lake obtain few alewives at other runs (despite the presence of several nearby).

Discussion

Cormorants are major predators of alewives at Bride Lake. We estimate that cormorants on Bride Lake consumed 20 687 (11 417–39 923) and 23 705 (13 083–45 747) adult alewives in 2005 and 2006, respectively, which represents 30% (17%–58%) and 18% (10%–35%) of the alewives spawning in Bride Lake in those years and 48% (27%–93%) of the overall mortality in 2005. The arrival of large flocks of cormorants at Bride Lake in spring is concurrent with the escapement of the largest schools of alewives. From our observations on the local cormorant diet, the diversity of fish in Bride Lake, and cormorant feeding strategies, we conclude that large flocks of cormorants use Bride Lake to exploit the high density of alewives there in spring.

Though cormorants are important predators of alewives at Bride Lake, our results suggest that they are not an immediate threat to alewife populations, both at Bride Lake and regionally. In the mid-1960s, when cormorants were largely absent from Connecticut, Kissil (1974) estimated that alewife spawning mortality at Bride Lake was 53%. This estimate was obtained from 2 years of visual counts of alewives entering and leaving Bride Lake at a fish ladder. Assuming that background mortality of alewives is density-independent, we can estimate the maximum potential mortality impact of cormorants by adding their consumption (20 687) to the 53% background rate (36 601). This approach estimates the hypothetical, completely additive mortality as 83% (57 289 alewives). This estimate is substantially higher (14 401 alewives) than the recorded mortality of 62% (42 888 ale-

wives). Comparing the recorded alewife mortality in 2005 with Kissil's estimate of background mortality suggests that only 6286 of the alewives consumed by cormorants are additive to background mortality. Based on a total consumption of 20 687 alewives, this result suggests that 70% of cormorant consumption is compensatory to background rates. Further, though cormorants consume a large proportion of spawning alewives, O'Gorman et al. (2004) have shown that alewives can produce very large year classes at low density. Thus, even a greatly reduced number of spawning adult alewives could produce a relatively large number of young of the year. This inference, combined with the mortality rate data from Bride Lake, strongly suggests that predation by cormorants is not the single cause of declining alewife escapement at Bride Lake.

Our observations also suggest that cormorants do not impact regional alewife populations. Cormorants are absent from other local spawning lakes (Dodge and Gorton ponds), and our diet analysis shows that consumption by all cormorants within foraging range of Bride Lake is no greater than that at Bride Lake alone. Even if cormorants from beyond the normal foraging range fed at Bride Lake (not supported by our observations), this pattern would indicate that the impact of cormorants along an even longer stretch of the Connecticut coastline was no greater than that at Bride Lake alone. Since cormorants do not appear to have greatly impacted the alewife population at Bride Lake, where the concentration of cormorants is extraordinary, we consider it very unlikely that they impact alewife populations elsewhere. Cormorants could impact alewife populations if their abundance at spawning sites were much greater than at Bride Lake. However, evidence from this study and observations at other sites suggest that is rarely the case.

While we do not see current cormorant predation as a threat to existing alewife populations, declining and highly variable alewife escapement combined with increasing predator abundance could undermine long-term management of alewife populations. Because generalist predators like striped bass and cormorants can switch food sources, their population dynamics are typically not sensitive to changes in any single prey item. The predation pressure imposed by cormorants and striped bass on alewives should remain constant, even as alewife populations continue to decline. Our results support this hypothesis, as an 87% change in alewife escapement in Bride Lake (2005 to 2006) was countered by only a 5% change in the average daily cormorant count.

Constant predation on declining alewife populations may undermine the alewife's ability to sustain itself. Hartman (2003) has shown that striped bass in the Hudson River can consume all of that river's annual production of river herring biomass. While O'Gorman et al. (2004) demonstrate that alewives can produce large year classes at low spawning stock density, we hypothesize that alewives will not be able to produce sustainable year classes below a critical spawner density. Given continuing alewife population declines, this scenario could occur at Bride Lake in years of particularly low alewife escapement, when cormorants could consume nearly all adult alewives. Such single-lake-scale events, repeated with enough frequency over time and across lakes, would greatly impact regional alewife populations. Thus, while our results show that cormorants pose no immediate threat to alewife populations, we suggest that double-crested cormorants, as generalist predators, could detrimentally impact regional alewife populations by exploiting local populations.

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Appendix A

Table A1 appears on the next page.

Table A1. Otolith length (OL) to total length (TL) regression parameters; TL to fresh weight (FW) regression parameters; and energy density (ED) estimates.

	OL to TL regression form: $TL = A \cdot OL + B$				TL to FW regressions form: $\log(W) = A + B[\log(TL)]$				ED estimates			
Species	*n*	*A*	*B*	R^2	*n*	*A*	*B*	R^2	*n*	Mean ED	SE	Reference[a]
Fundulus heteroclitus	27	49.9	–9.17	0.90	31	–5.39	3.28	0.98	26	4.98	0.07	
Labridae spp.	13	88.4	–70.2	0.94	11	–4.67	2.92	0.97	5	5.12	0.13	
Peprilus triacanthus	7	27.1	8.97	0.98	6	–5.93	3.48	0.94	–	–	–	
Stenotomus chrysops	6	33.2	–31.8	0.99	5	–6.08	3.58	0.96	2	5.72	0.28	
Alosa pseudoharengus	31	95.5	–68.1	0.97	369	–5.3	3.12	1	20	5.86	0.15	
Morone americana	14	28.7	–57.2	0.95	1706	–1.43	2.89	0.92	4	3.79	0.19	1
Menidia menidia	6	58.3	0.99	0.98	10	–4.65	2.75	0.97	—	—	—	
Anguilla rostrata	3	193.1	–84.8	0.89	48	–5.69	2.98	0.99	—	—	—	2
Perca flavescens (7)	5	24.2	25.6	0.98	372	–3.76	2.43	NA	—	—	—	3[c]
Myoxocephalus aeneus[b]	51	1.42	–2.8	0.97	119	–4.93	3.03	0.99	—	—	—	4
Paralichthys spp.	7	68.9	–68	0.91	NA	–5.25	3.1	0.99	—	—	—	5, 6
Oncorhynchus mykiss	13	91.8	–52	0.86	121	–6.3	2.76	NA	—	—	—	7
Morone saxatilis	4	41.9	–99.8	0.98	1364	–5.08	3.07	NA	—	—	—	
Combined demersal[d]	—	—	—	—	—	—	—	—	21	4.94	0.17	
Combined freshwater[e]	—	—	—	—	—	—	—	—	10	4.94	0.23	

[a]References are as follows: (1) Marcy, B.C., Jr., and Richards, F.P. 1974. Age and growth of the white perch, *Morone americana*, in the lower Connecticut River. Trans. Am. Fish. Soc. **103**: 117–120. (2) Carlander, K.D. 1950. Handbook of freshwater fishery biology. Wm. C. Brown Company, Dubuque, Iowa. (3) Carlander, K.D. 1997. Handbook of freshwater fishery biology. Vol. III. Iowa State University Press, Ames, Iowa. (4) Roseman, E.F., Tomichek, C.A., Maynard, T., and Burton, J.A. 2005. Relative abundance, age, growth, and fecundity of grubby, *Myoxocephalus aeneus*, in Niantic River and Niantic Bay, Long Island Sound. J. Sea Res. **53**: 309–318. (5) Grimes, B.H., Huish, M.T., Kerby, J.H., Moran, D., and Pendleton, E. 1974. Summer and winter flounder. USFWS Biological Reports, **82** (11.112). (6) Powell, A.B. 1974. Biology of the summer flounder, *Paralichthys dentatus*, in Pamlico Sound and adjacent waters, with comments on *P. lethostigma* and *P. albigutta*. M.S. thesis, University of North Carolina, Chapel Hill, N.C. (7) Carlander, K.D. 1969. Handbook of freshwater fishery biology. Vol. I. Iowa State University Press, Ames, Iowa.

[b]Form: $\ln(TL) = A \cdot \ln(OL) + B$.

[c]Species include *Labridae* spp. ($n = 5$), *Microgadus tomcod* ($n = 4$), *Gadus morhua* ($n = 2$), *Stenotomus chrysops* ($n = 2$), *Centropristis striata* ($n = 7$), and *Pseudopleuronectes americanus* ($n = 1$).

[d]Species include *Lepomis macrochirus* ($n = 7$) and *Fundulus diaphanous* ($n = 3$).

[e]Length adjusted to convert TL to fork length.

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Appendix B. Bioenergetic modeling approach: overview

We calculated cormorants' seasonal consumption of alewives using bioenergetic modeling. We first estimated the total daily energy intake of the cormorant population from literature energy estimates and empirical population counts. We converted daily energy intake to total daily alewife consumption based on the energy density of prey items and the diet proportion composed of alewives. We summed daily consumption estimates across all alewife spawning dates to calculate total seasonal consumption.

Because all model inputs incorporate some uncertainty, we estimated maximum and minimum values for each parameter. Our methodology for estimating these maximum and minimums is described below.

I. Calculating total daily cormorant energy intake

Overview

We calculated the daily energy intake of a single cormorant by multiplying the estimated daily per-cormorant energy expenditure by a digestive efficiency ratio. The total energy intake of cormorant populations was then estimated by multiplying per-cormorant energy intake by daily estimates of cormorant population size.

Estimating per cormorant energy expenditure

We used the all seabirds field metabolic rate (FMR) regression of Ellis and Gabrielsen (2002) to estimate the daily energy expenditure (DEE) per cormorant as follows:

$$DEE = 16.69\ M^{0.651}$$

where M is the mass (g) of a cormorant.

Based on an estimated cormorant mass of 2051 g, this regression calculated FMR at 2391 kJ·cormorant^{-1}·day^{-1}. We used the standard errors provided by Ellis and Gabrielsen (2002), together with estimates of minimum and maximum cormorant mass (Table 1), to create a range of potential daily energy expenditures (1581–3817).

Digestive efficiency

To calculate energy intake per cormorant per day, we divided the estimated daily energy expenditure (FMR) by Brugger's (1993) empirically determined cormorant digestive efficiency of 0.779. To create a range of potential values, we used Brugger's minimum DE estimate (for bluegill; 0.75) and maximum DE estimate (for channel catfish (*Ictalurus punctatus*); 0.79).

Cormorant population size

We estimated the total daily energy intake by cormorant populations by multiplying the per-cormorant energy intake by the number of cormorants in each population. We interpreted linearly between our known counts to create daily cormorant population size estimates for Bride Lake and the local population (see main text for counting methodology). We created maximum and minimum population size estimates by varying daily counts ± 10% from the actual counts for Bride Lake and ± 20% for the local cormorant population.

II. Estimating daily alewife consumption

Overview

From the total daily cormorant energy intake, we calculated fish consumption (in g) by dividing the total energy intake (in kJ) by the estimated energy density of prey items (in kJ·g^{-1}). We then estimated alewife consumption (in g) by multiplying total fish consumption by the cormorant diet proportion composed of alewives. The count of alewives consumed was calculated by dividing the total estimated mass of alewife eaten by the average mass of an alewife.

Energy density of prey items

We empirically estimated the energy density (ED) of each prey taxon from whole fish wet weight:dry weight ratios and the equations of Hartman and Brandt (1995) (Appendix A). Measured fish were sampled by beach and purse seine, hook and line, and minnow traps, and fish were collected from locations where cormorants from Long Ledge were observed feeding. Alewives were collected directly from Bride Lake at the peak of the alewife run. In all cases, fish sampling was concurrent with cormorant diet sampling and population estimation. We obtained empirical ED estimates for species composing 88% of the cormorant diet.

For cormorants feeding at Bride Lake, prey ED was modeled as equal to our ED estimate for alewife, 5.92 kJ·g^{-1}. For the local cormorant population, prey ED was estimated as the average energy density of all prey, weighted by proportion in the cormorant diet. For dates where diet samples were available, we calculated these estimates directly from diet proportions. Linear interpolation between known dates was used to create daily weighted ED averages for dates with no diet samples.

A range of maximum and minimum energy density estimates was calculated based on the standard error of our ED measurements.

Diet proportion

At Bride Lake, the proportion of the diet composed of alewives was assumed to always equal one (see note in main body of paper). For the local cormorant population, diet proportion was determined directly from cormorant diet samples (see main text for detail on methodology). For dates with no diet samples available, linear interpolation between known samples was used to create daily diet proportions.

A range of maximum and minimum alewife diet proportions was created for the local cormorant population by varying the daily proportion of alewives in the diet ± 10%.

Mass of alewives

The mass of an alewife was calculated from measurements of alewives sampled entering Bride Lake. Alewives were collected from Bride Lake via established weirs used for population estimation. If possible, alewife mass was obtained from chilled fish within 4 h of mortality. Some fish were frozen (again, within 4 h) and then weighed. A range of possible alewife masses was created based on the standard error of our Bride Lake sample.

III. Other models

Without detailed behavioral data, cormorant energy intake can be estimated by three methods. One combines an estimate of basal metabolism with an FMR:BMR (basal metabolic rate) ratio to estimate the per-cormorant daily energy intake (e.g., Kendeigh et al. 1977). A second method avoids the issue of prey energy density by estimating cormorant consumption as a percentage of body weight (e.g., 20%, Rudstam et al. 2004; 22%, Glahn and Brugger 1995). Each of these two models produced consumption estimates less than 20% different than the midpoint consumption estimate and within the range of standard error for the FMR-based model of Ellis and Gabrielsen (2002).

In short, we chose to use the FMR model because it maximized the potential insights from available data without sacrificing precision. Unlike a percentage of body weight model, the FMR model enables the modeler to adjust consumption estimates based on shifts in prey energy, like that which occurs when cormorants switch from alewives to lower energy density food sources (see Appendix A for magnitude of difference). Additionally, the FMR model incorporates less uncertainty than the basal metabolism model, which requires an FMR:BMR multiplier — a highly sensitive model parameter.

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Factors influencing the achievement of steady state in mercury contamination among lakes and catchments of south-central Ontario

R. Brad Mills, Andrew M. Paterson, Jules M. Blais, David R.S. Lean, John P. Smol, and Greg Mierle

Abstract: Mercury (Hg) concentrations in recent (0.5–1 cm) and preindustrial (>30 cm) sediments were examined across lakes in south-central and eastern Ontario, Canada (45.53 N, 82.41 W to 44.15 N, 76.25 W), to determine whether Hg exported from watersheds is at steady state with atmospheric deposition. An examination of headwater lakes revealed that Hg enrichment was not uniform among watersheds but that the enrichment factor (EF = $[Hg]_{present\ day}/[Hg]_{preindustrial}$, standardized for organic matter) decreased as a function of drainage ratio (A_d/A_o, $watershed_{area}/lake_{area}$). Furthermore, the model fit was improved after accounting for differences in sulfate concentrations and pH among lakes: $EF = (A_d/A_o)^{-15.98} - 0.07(SO_4^{2-}) - (3.55(pH_{ca.3}))$ ($R^2 = 0.458$, $p = 0.0001$). Hg concentrations in preindustrial sediments of headwater lakes showed a positive linear relationship with drainage ratio (partial $t = 4.83$, $p < 0.0001$, $n = 66$) that was strengthened following an adjustment for mean annual runoff (MAR) ($[Hg]_{preindustrial} = 0.011 \pm 0.002(A_d/A_o) + 0.0008 \pm 0.0003(MAR)$ ($R^2 = 0.108$, $F_{[1,66]} = 8.01$, $p = 0.006$)). Our results suggest that Hg export from watersheds may be currently lagging behind atmospheric Hg deposition, in which case, Hg export would increase into the future, even as Hg deposition from the atmosphere stabilizes.

Résumé : Nous avons mesuré les concentrations de mercure (Hg) dans les sédiments récents (0,5–1 cm) et préindustriels (>30 cm) dans des lacs répartis dans tout le centre-sud et l'est de l'Ontario, Canada (45,53 N, 82,41 O à 44,15 N, 76,25 O) afin de déterminer si le Hg exporté des bassins versants est en équilibre avec les retombées atmosphériques. Un examen des lacs d'amont des bassins versants indique que l'enrichissement en Hg n'est pas uniforme dans tous les bassins, mais que le facteur d'enrichissement (EF) ($[Hg]_{actuelle}$ / $[Hg]_{préindustrielle}$; corrigé pour tenir compte de la matière organique) décroît en fonction du rapport de drainage (A_d / A_o; $bassin_{surface}$ / $lac_{surface}$). De plus, l'ajustement du modèle s'améliore si on tient compte des différences de concentrations de sulfates et de pH entre les lacs: $EF = (A_d/A_o)^{-15.98} - 0.07(SO_4^{2-}) - (3.55(pH_{ca.3}))$ ($R^2 = 0.458$, $p = 0.0001$). Il existe une relation linéaire positive entre les concentrations de Hg dans les sédiments préindustriels des lacs d'amont et le rapport de drainage (t partiel = 4,83, $p < 0,0001$, $n = 66$) qui est renforcée si on fait un ajustement pour tenir compte du ruissellement annuel moyen (MAR) ($Hg_{préindustriel} = 0,011 \pm 0,002\ (A_d/A_o) + 0,0008 \pm 0,0003(MAR)$ ($R^2 = 0,108$, $F_{[1,66]} = 8,01$, $p = 0,006$)). Nos résultats laissent croire que l'exportation de Hg des bassins versants peut être actuellement décalée par rapport aux retombées atmosphériques de Hg; dans ce cas, l'exportation de Hg devrait augmenter dans le futur, même s'il y a une stabilisation des retombées de Hg de l'atmosphère.

[Traduit par la Rédaction]

Introduction

Mercury (Hg) is globally distributed because it is ubiquitous in surficial geology at varying concentrations and it has a long atmospheric residence time (Mason et al. 1994; Fitzgerald et al. 1998). Although natural emissions contribute to the pool of atmospheric Hg and its subsequent deposition, the contamination of surface waters has increased dramatically in the past century owing to anthropogenic sources (Fitzgerald et al. 1998; Hermanson 1998; Schuster et al. 2002). Lake sediment studies in North America report increases in Hg deposition of two to three times the historical background (Swain et al. 1992; Engstrom and Swain 1997; Schuster et al. 2002), although regional differences in Hg enrichment exist owing to variability in site-specific geology and geographical variation in the distribution of industrial emissions. Such increases have been confirmed by glacial ice cores (Schuster et al. 2002). The increase in industrial

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activity, and subsequent global release and contamination by Hg over the past century, has left a legacy of largely unknown repercussions for aquatic ecosystems. Present levels of Hg contamination in many north-temperate lakes exceed guidelines for the protection of wildlife and the human consumption of sport fish (Basu et al. 2005; Scheuhammer et al. 2008).

Despite regulatory controls that have reduced industrial emissions (Sang and Lourie 1997; Innanen 1998; Trip et al. 2004), atmospheric Hg concentrations have not diminished significantly over the last decade in remote areas (Trip et al. 2004; Vanarsdale et al. 2005). Temme et al. (2007) found that the largest decline in atmospheric concentrations over the last decade were in close proximity to large urban areas (17% in Pointe Petre (Toronto, Ontario) and 13% in St. Anicet (Montréal, Quebec)). In part, this may be explained by complex patterns of deposition and reemission of Hg from the earth's surface to the atmosphere that may impede a return to preindustrial conditions in rural areas (Lee et al. 1998; Lindberg et al. 1998; Gustin et al. 2004).

In aquatic ecosystems, an additional barrier to ecosystem recovery from Hg contamination may be that terrestrial environments are not in steady state with surface waters (Swain et al. 1992; Meili et al. 2003). Under a steady-state model, the amount of Hg entering aquatic ecosystems increases proportionately with watershed size and the drainage ratio (A_d/A_o). Meili (1995), however, reported nonlinear correlations between Hg enrichment and drainage ratios in Swedish lake ecosystems. A higher relative enrichment was recorded in sediments of lakes with small watersheds (four- to six-fold versus two- to three-fold in lakes with large watersheds), suggesting that steady state had not been achieved (Meili 1995). Thus, in this example, terrestrial export may lag behind declines in atmospheric deposition owing to the storage and accumulation of Hg in watersheds (Lindqvist et al. 1991; Meili et al. 2003; Perry et al. 2005). Consequently, it may take years to decades before significant declines in Hg release to surface waters are realized.

Over time, the relationship between Hg export and watershed characteristics may be further complicated by regional stressors such as acid deposition. Experimental studies have shown that Hg export is largely dependent on pH. Following liming, Parkman and Munthe (1998) reported a 67% decline in Hg export relative to a reference catchment. Similarly, in a study of 25 boreal lakes in Sweden, Meili et al. (1991) measured Hg concentrations that were twice as high in acidic lakes (pH 5) than in circumneutral lakes. Both studies attributed their findings to increased leaching of Hg-loaded dissolved organic carbon (DOC) from soils at lower pH. However, increased concentrations of volatile Hg species in high-pH lakes may, in part, have contributed to this observation (Vandal et al. 1991). Estimates of evasional flux as high as 45% of dissolved Hg have been made during experimental isotope additions to the epilimnion of Lake 658 (Experimental Lakes Area, northwestern Ontario) (Southworth et al. 2007), although volatization of ambient Hg is likely lower and has been reported at 14% of the atmospheric flux (Vandal et al. 1991).

In many regions, direct measurements of Hg deposition are unavailable or have only been recorded in detail during the last decade (Vanarsdale et al. 2005). Because Hg exhibits a high affinity for organic matter, however, a large fraction of Hg entering surface waters is delivered to lake sediments (Boyle 2001), and paleolimnological techniques may be used to reconstruct long-term trends in Hg contamination. Sediment studies of Hg deposition in remote areas around the globe show similar increases since the preindustrial era, despite variability in catchment and basin characteristics (Engstrom and Swain 1997; Landers et al. 1998; Bindler et al. 2001). Furthermore, although Hg in lake sediments is potentially susceptible to postdepositional processes (e.g., diagenesis and oxidation–reduction) that may confound the relationship between actual conditions and those in historical records (El Bilali et al. 2002; Telmer and Desjardins 2004), it has been estimated that only 2%–10% of the Hg deposited to sediments is redistributed even under low sedimentation rates (Gobeil and Cossa 1993). Furthermore, three case studies of known Hg deposition to sediments suggested that under moderate sedimentation rates, redistribution may be considered negligible in comparison with Hg loading (Lockhart et al. 2000).

The primary objective of this study is to determine whether or not watersheds in south-central and eastern Ontario are in steady state with respect to Hg deposition and export. Specifically, we examine the relationship between A_d/A_o and Hg concentrations in present-day and preindustrial sediment samples of headwater lakes in south-central and eastern Ontario. Predictive models are constructed to assess the degree to which A_d/A_o influences Hg concentrations in lake sediments, independent of regional differences in hydrology or the geographic distance between sites. We test the null hypothesis that Hg retention in watersheds has not changed significantly over time by comparing separate models generated with present-day and preindustrial sediment Hg concentrations. This hypothesis would be supported if present-day and preindustrial sediment Hg concentrations show similar, proportional increases in A_d/A_o. If present-day and preindustrial Hg concentrations increase proportionally with drainage ratio, it would suggest that Hg retention in watersheds has not changed during this period.

Secondly, we test the hypothesis that anthropogenic acidification may have altered the relationship between A_d/A_o and sediment Hg concentrations. The watersheds in this study span a geological gradient of buffering capacity (i.e., lakes on and off the Precambrian Shield), thus providing a natural test of this hypothesis. We examined the relationship between Hg enrichment in lake sediments since preindustrial times and measured lakewater pH and DOC in headwater lakes for which monitoring data were available. Based on the current understanding of acidity and Hg export, we expect that in watersheds that are sensitive to anthropogenic acidification, Hg export will have increased over time, resulting in larger increases in sediment Hg concentrations versus drainage ratio since the preindustrial era.

Materials and methods

Study sites

Mercury concentrations were measured in preindustrial and present-day lake sediments from approximately 202 lakes in Ontario, Canada, although modelling was restricted to 68 headwater systems to reduce confounding variation in

lake chemistry and biology associated with lake order (Table 1) (Quinlan et al. 2003). The lakes span gradients of hydrological and geological characteristics and cross the major geological boundary separating the Canadian Precambrian Shield (granitic geology) from the limestone-based Trenton and Beekmantown formations in eastern Ontario (Chapman and Putnam 1996) (Fig. 1). The majority of the study lakes lie upon the Grenville Province, which is characterized by rugged topography and is underlain with generally shallow tills and soils with localized areas of thicker clay, sand, and gravel deposits (Jeffries and Snyder 1983). Lakes on the southern border of the Canadian Shield, including lakes on the Bruce Peninsula and south of Georgian Bay, lie upon the sedimentary rocks of the Western St. Lawrence Lowlands, which include regions of agricultural activity (i.e., pockets of forest surrounded by cultivated land with deeper glacial till). Lakes within Killarney Park are surrounded by quartzite ridges, which provide little to no buffering capacity to acidic precipitation. These lakes are generally acidic and largely influenced by the local geology (Snucins et al. 2001). Most of the study lakes lie within the Great Lakes – St. Lawrence Forest Region (Rowe 1977) and land coverage is dominated by mixed forest, mainly coniferous, followed by dense deciduous forest and sparse deciduous forest (refer to Hall and Smol 1996). Much of the study area, in particular southern Ontario, is subjected to acid deposition from long-range sources according to the Canadian acid deposition science assessment (Morrison and Carou 2004). Morphometric data (watershed area, lake area, slope of basin, and length of tributaries) and hydrological data (mean annual precipitation, runoff, evaporation, and snowfall) were delineated for watersheds using digital elevation models to determine watershed boundaries. GIS layers (i.e., hydrology, land cover) were compiled using Ontario Flow Assessment Techniques, a GIS platform produced by the Ontario Ministry of Natural Resources (Chang et al. 2002). Since the digital elevation models contain vector information, lake order was established by observing upstream lakes.

Field and laboratory methods

Lake sediments were collected using Lucite Glew (1989) gravity corers in replicate at the deepest point of each lake between 2001 and 2003. Sediment cores were sectioned on the lakeshore using a Glew (1989) extruder into Whirlpak bags and stored in coolers for transport back to the laboratory. Samples were refrigerated at the Paleoecological Environmental Assessment and Research Laboratory at Queen's University (Kingston, Ontario) at 4 °C in the dark until analysis.

In this study, two sediment sections were examined in each core: the top 0.5–1.0 cm (present-day lake conditions) and a 0.5–1.0 cm interval taken at a minimum core depth of 30 cm. Although the precise date of the bottom sample from each lake is not known, dating of lake sediments using ^{210}Pb from many south-central Ontario lakes, in this study and supported by others, indicates that the preindustrial time period is typically reached at a sediment depth of 15–20 cm (Evans 1986; Clerk et al. 2000). Paleoenvironmental reconstructions from other Precambrian Shield regions indicate similar results (e.g., Adirondacks: Charles 1985; Norton and Kahl 1991; Cumming et al. 1992; Sudbury: Dixit et al. 2002), as do results from near-surface and deep sediments in 30 lakes from various regions of our study area.

Mercury concentrations were determined using solid-phase thermal desorption atomic fluorescence spectroscopy (SP-3D; Nippon Instruments Corp., Osaka, Japan). Sediments were dried at 60 °C and ground to a fine powder with a mortar and pestle and approximately 30 mg of the powder was embedded in activated alumina powder and placed into a ceramic holder. The elemental Hg released from this process was trapped by gold amalgamation. Subsequently, the Hg was thermally desorbed and then detected by absorption at 253.7 nm. Certified reference material (MESS-3, NIST 1603) was used to calibrate the response.

The variability in Hg concentrations was quantified for duplicate samples, several samples within a single core (0.5–1 cm), and adjacent cores from the lake bottom prior to developing models. The relative standard error in Hg concentrations for analytical duplicates was 2.6%, while the error among adjacent cores was 5.9%.

Unless otherwise stated, Hg concentrations presented in this study were expressed relative to sediment organic matter content as determined through mass loss on ignition. Organic matter content was determined using the difference in sediment weight after sequential heating regimes (Heiri et al. 2001). Organic matter content was inferred from the mass loss on ignition between freeze-dried sediment and following combustion at 550 °C.

Data used for water chemistry were gathered from Ontario Ministry of the Environment long-term lake monitoring databases as well as from Hall and Smol (1996), Reavie and Smol (2001), and Dixit et al. (2002). Lakewater sampling (Locke and Scott 1986) and chemical analyses (Jeffries and Snyder 1983; Janhurst 1998) were performed by the Ontario Ministry of the Environment. In most instances, water chemistry from south-central Ontario lakes represents multiple measurements of volume-weighted whole-lake composites. Some lakes were sampled on a biweekly basis; others were sampled monthly or bimonthly during the ice-free seasons. Water from lakes in eastern Ontario and on the Bruce Peninsula was collected as surface or epilimnetic composites in the spring and late summer only. For more details regarding sediment and chemical sampling procedures, please see Hall and Smol (1996), Reavie and Smol (2001), and Dixit et al. (2002).

Data analysis

In this study, we constructed models from Hg concentrations measured in profundal sediment cores. Prior to constructing these models, we assessed sources of variation in our analyses using analysis of variance (ANOVA). Variation was quantified at various levels of analysis, including (*i*) Hg concentrations in profundal sediments within and among lakes and (*ii*) the precision of Hg concentrations from replicate samples.

Statistical analysis was performed in S-Plus version 6.2 (with additional modules) (Insightful Corporation, Seattle, Washington) and in SigmaStat version 3.0 (Systat Software Inc., Chicago, Illinois). Differences between sediment Hg concentrations as well as water chemistry (e.g., lake pH) among geological regions were tested using an ANOVA on

Table 1. Physical and chemical properties of the 68 headwater lakes used in this study.

Lake	Latitude (°N)	Longitude (°W)	Watershed area (km²)	Lake area (km²)	A_d/A_l	Runoff (mm·year⁻¹)	Precipitation (mm·year⁻¹)	pH	DOC	Hg total (μg·g⁻¹ organic matter) Present day	Preindustrial	Increase	RSE	No. of cores
Acid	46.03	–81.44	4.4	0.2	23	506	774	—	—	1.08	0.63	1.7	—	1
Arran	44.50	–81.24	24	4	7	471	860	8.6	9.7	0.15	0.08	1.9	8.8	2
Bass	44.72	–80.99	6	1	12	471	895	8.6	3.1	0.40	0.24	1.7	—	1
Bass	45.12	–79.71	5	1	6	493	933	6.3	4.4	0.91	0.41	2.2	—	1
Beaver	44.77	–78.27	80	2	40	321	823	6.4	4.9	0.97	1.78	0.5	4.7	2
Bell	46.13	–81.23	19	1	23	439	933	8.5	5.5	0.75	0.34	2.2	—	1
Berford	44.81	–81.19	21	4	5	476	824	8.5	5.8	0.15	0.16	1.0	0.3	2
Brewster	44.34	–80.31	2	0	7	431	809	8.8	6.2	0.24	0.24	1.0	34.8	2
Bruce	45.18	–79.66	3	1	3	495	936	6.8	4.0	0.66	0.38	1.7	—	1
Cameron	45.23	–81.55	9	2	6	500	764	8.5	5.8	0.56	0.18	3.1	1.9	2
Carlyle	46.05	–81.29	9.0	1.6	6	502	744	—	—	0.88	0.47	1.9	—	1
Chub	45.21	–78.98	3	0	9	495	930	5.6	4.9	0.78	0.30	2.6	—	1
Collins	44.35	–76.45	37	3	11	—	—	7.3	6.0	0.36	0.12	2.9	2.2	3
Crosson	45.09	–79.03	6	1	10	485	939	5.6	4.5	0.81	0.31	2.6	—	1
Crowe	44.48	–77.72	1444	876	2	—	—	7.3	5.1	0.88	0.32	2.7	7.6	3
Crystal	44.75	–78.49	41	4	9	326	836	7.7	5.5	0.60	0.29	2.0	4.5	2
Dankert	44.21	–81.06	1	0	6	471	889	9.1	13.8	0.32	0.07	4.3	5.0	2
David	46.13	–81.28	15.1	4.1	4	503	754	—	—	1.32	0.29	4.6	—	1
Dog	44.43	–76.35	62	5	13	—	—	8.2	5.0	0.55	0.49	1.1	3.1	3
Eagle	45.13	–78.51	40	7	6	—	—	7.9	4.4	0.82	0.23	3.6	14.7	3
East Bass	45.87	–81.93	25	3	10	517	754	8.5	5.4	0.30	0.25	1.2	22.2	2
Eugenia	44.33	–80.52	138	6	21	444	838	8.7	4.8	0.42	0.51	0.8	—	1
Farren	44.77	–76.49	12	2	7	354	712	8.2	4.0	0.40	0.18	2.3	—	1
Gillies	45.28	–81.32	13	2	6	—	—	8.6	5.1	0.66	0.24	2.7	48.9	2
Gould	44.59	–81.21	10	2	5	425	796	8.2	3.4	0.75	0.17	4.3	3.4	2
Gravenhurst	44.93	–79.40	11	2	6	—	—	7.2	3.9	1.43	0.56	2.6	—	1
Grippen	44.50	–76.16	20	191	0	456	728	8.1	5.0	0.89	0.18	4.9	4.3	3
Haliburton	45.18	–78.42	144	10	14	468	871	7.0	3.5	1.38	0.51	2.7	—	1
Hammel	45.19	–79.47	13	2	9	495	938	7.2	4.9	0.87	0.49	1.8	—	1
Harp	45.38	–79.13	5	1	8	504	906	6.4	3.7	0.84	0.51	1.7	—	1
Hines	44.42	–80.74	1	0	10	448	887	8.5	4.7	0.36	0.11	3.2	7.8	2
Inverary	44.38	–76.46	10	1	13	504	807	7.5	6.5	0.51	0.42	1.2	9.1	3
Irish	44.27	–80.64	3	0	13	443	935	9.0	5.5	0.31	0.21	1.5	3.3	3
Ishmael	46.11	–81.60	11.7	0.7	16	509	780	—	—	0.96	0.43	2.2	—	1
Kagawong	45.84	–82.28	105	55	2	513	760	8.6	3.8	0.48	0.40	1.2	—	1
Kennisis	45.24	–78.59	134	14	9	489	902	6.3	2.8	1.29	0.46	2.8	—	1
Kerr	45.91	–83.08	3	0	15	503	785	8.6	11.4	0.25	0.30	0.8	—	1
Knowlton	44.47	–76.61	11	2	6	422	811	8.2	3.9	0.90	0.16	5.6	3.1	3
L. Clear	45.40	–79.00	4	0	39	—	—	6.8	2.8	0.51	0.40	1.3	3.5	3

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Table 1 (*concluded*).

Lake	Latitude (°N)	Longitude (°W)	Watershed area (km²)	Lake area (km²)	A_d/A_o	Runoff (mm·year⁻¹)	Precipitation (mm·year⁻¹)	pH	DOC	Hg $_{total}$ (μg·g⁻¹ organic matter) Present day	Preindustrial	Increase	RSE	No. of cores
L. Kennisis	45.25	–78.58	67	2	29	477	873	6.1	3.7	0.37	0.79	0.5	—	1
Leggat	44.70	–76.72	12	2	6	327	777	7.6	3.6	0.45	0.11	4.3	3.2	2
Lily	45.88	–83.09	6	2	3	503	785	8.8	7.3	0.19	0.11	1.8	0.6	2
Limerick	44.86	–77.61	181	7	24	389	757	7.9	4.3	0.80	0.29	2.8	4.6	2
Long	45.02	–78.39	8	3	3	475	878	8.8	11.6	0.27	0.23	1.2	2.3	2
Lorne	45.78	–82.61	27	1	22	507	747	8.8	10.2	0.47	0.54	0.9	4.7	1
Loughborough	44.44	–76.39	58	7	8	480	795	7.5	3.6	0.67	0.25	2.7	—	1
Low	46.10	–81.57	9.7	0.3	29	508	773	—	—	1.59	0.34	4.7	—	1
Manitou	45.72	–81.98	130	106	1	515	752	8.5	2.9	0.66	0.25	2.6	4.7	2
Mc Cullough	44.35	–80.92	32	1	50	451	917	8.5	3.8	0.39	0.23	1.7	1.1	2
Mindemoya	45.72	–82.22	64	36	2	513	752	8.6	3.2	0.32	0.48	0.7	1.2	2
Muskoka Bay	44.95	–79.40	11	2	5	—	—	7.1	3.9	0.31	0.75	0.4	—	1
Nameless	45.82	–82.44	10	1	16	511	750	8.7	3.6	0.81	0.92	0.9	0.2	2
Newboro	44.62	–76.30	375	18	20	—	—	8.0	4.8	0.30	0.20	1.5	—	1
Partridge	46.09	–81.29	0.4	0.1	3	502	744	—	—	1.20	0.32	3.7	—	1
Pike	44.80	–76.33	60	3	19	372	711	8.4	5.5	0.58	0.30	1.9	6.2	2
Pike	45.88	–81.97	32	2	15	516	754	8.5	6.0	0.39	0.31	1.3	2.6	2
Redstone	45.16	–78.55	190	11	17	480	885	6.5	3.0	1.21	0.59	2.0	—	1
Salmon	44.83	–78.44	7	2	4	339	840	7.8	3.7	0.59	0.15	3.8	8.4	3
Silver	44.08	–81.41	11	1	20	522	814	8.9	6.1	0.11	0.12	0.9	1.5	3
Skootamatta	44.80	–77.22	132	8	16	374	754	6.5	5.1	0.79	0.44	1.8	0.3	3
Solitaire	45.40	–79.01	3	1	2	511	910	6.7	2.1	0.72	0.22	3.3	—	1
Soyer's	45.01	–78.61	47	3	14	478	881	7.0	5.5	1.02	0.51	2.0	—	1
Stone's	45.81	–82.50	15	1	28	510	750	8.4	5.2	0.62	0.39	1.6	1.6	2
Tallan	44.84	–78.05	4	0	9	388	815	7.8	5.4	0.41	0.14	3.0	1.5	3
Three Mile	45.17	–79.45	127	6	20	—	—	7.1	6.4	1.06	0.90	1.2	—	1
Tobacco	45.87	–82.45	15	2	7	511	750	8.7	3.9	0.64	0.40	1.6	—	1
Walker	45.37	–79.09	2	1	3	507	909	6.7	3.4	0.97	0.34	2.8	—	1
West Bass	45.91	–83.18	1	0	7	503	793	9.1	10.1	0.25	0.22	1.1	10.8	3
Wilcox	44.23	–80.56	1	0	5	456	914	8.4	5.8	0.40	0.23	1.8	1.4	3
Williams	44.40	–80.83	7	1	13	463	924	8.4	2.9	0.42	0.30	1.4	—	1

Note: Hydrology was interpolated among meteorological stations using GIS. Lakewater pH and dissolved organic carbon (DOC) concentrations represent samples collected during the ice-free seasons and averaged over several years. RSE, relative standard error.

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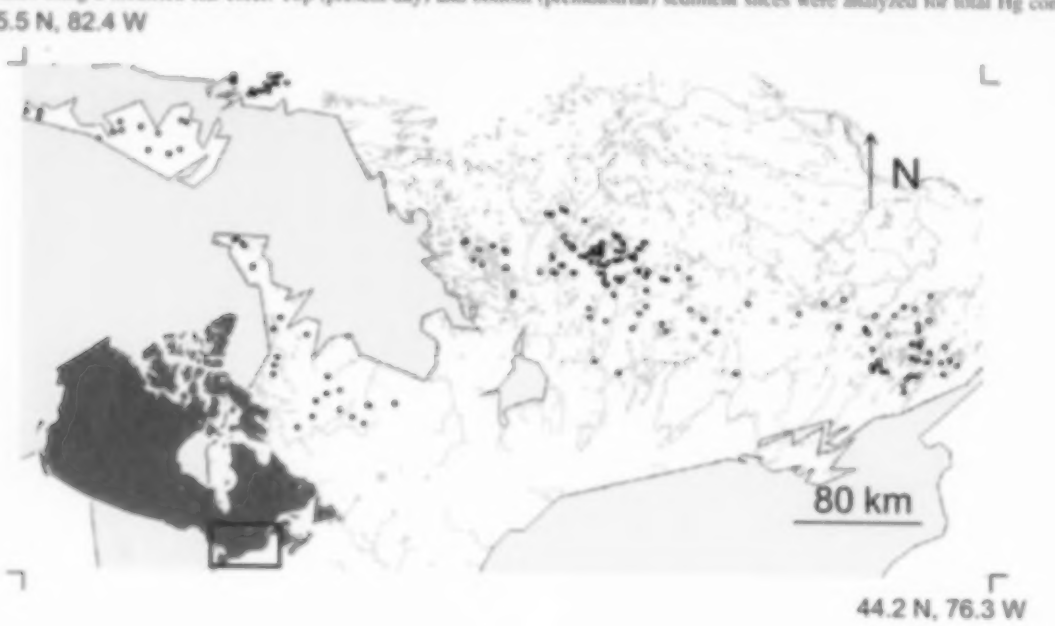
Fig. 1. Location of the study lakes in central and eastern Ontario, Canada (45.53 N, 82.41 W to 44.15 N, 76.25 W). Sediment was collected from 202 lakes using a modified KB corer. Top (present-day) and bottom (preindustrial) sediment slices were analyzed for total Hg content.



ranks. Nonparametric multiple comparisons were performed using a Holm–Sidak test. Where no statistical difference was established among the geological regions (i.e., sites on and off the Precambrian Shield) using ANOVA, data were pooled for subsequent analyses. Otherwise, data were grouped according to geological region.

Spatial analysis was performed to assess the degree of autocorrelation among lake sediments resulting from the geographic distance between sites. Semivariograms were constructed assuming that there would be local sources of variation in sediment Hg concentrations standardized for organic matter. This was achieved by setting a maximum radius for estimating variance to an Euclidean distance value of 10 from the lake location. For the purposes of this study, we chose to use an isotropic variogram, which assumes a symmetrical change in variation with distance from a prediction point (Deutsch and Journel 1992). The semivariance is equal to the sum of squared differences divided by $2nh$, where h is the distance between lakes and n is the number of paired lakes at each distance of h. Spatial analysis was conducted using the GSTAT module in S-Plus (Pebesma 2001).

Following an examination of variance in Hg concentrations as a function of distance using semivariograms, models were constructed using the drainage ratio A_d/A_o as a predictor of preindustrial and present-day Hg concentrations (nanograms per gram of C_{org}), where C_{org} is the organic matter content of the sediment samples. Linear models were tested for parametric assumptions and corrected for runoff by including mean annual runoff (MAR) in the models. Where spatial autocorrelation was apparent among sediment Hg concentrations, we included a cubic spline model of latitude and longitude. The significance of each model parameter was examined using the residual sum of squares difference. In the case of confounding factors (e.g., MAR), partial residuals were used to access the importance and form of the relationship among independent and dependent variables using S-Plus (Larsen and McCleary 1972). The hypotheses were tested after removing the proportion of variance in sedimentary Hg concentrations attributable to confounding variables (i.e., pH and sulfate concentration), as we were interested only in the relationship between drainage ratio and Hg concentrations for the first hypothesis and pH for the second hypothesis and not the interaction among predictor variables. To reduce the influence of other possible factors that may be correlated with landscape position (Quinlan et al. 2003), we restricted tests of our hypotheses to data from headwater lakes. In testing the second hypothesis, several lakes (n = 12) were missing data for sulfate monitoring and so the data set was reduced to 54 lakes.

Results

Lake sediments are spatially heterogeneous mixtures of mineral and organic matter. These characteristics may vary both in their location within a lake (Evans 1986) and vertically within sediment cores (El Bilali et al. 2002). Furthermore, Hg concentrations may vary considerably between littoral and profundal sediments (Evans 1986). However, our assessment of sources of variation in Hg concentrations indicates that most of the variation occurred among lakes ($F_{[1,82]}$ = 170.28, $p < 0.001$) with nonsignificant variability among cores within lakes ($F_{[1,82]}$ = 1.317, p = 0.25) (Table 2). Our examination of within-lake replication only considers cores from the deepest basin of each lake and makes no attempt at estimating whole-lake burdens for Hg. Prior research suggests that within-lake variability can be

Table 2. ANOVA of Hg concentrations among various stages of measurement.

Attribute	df	Sum of squares	Mean square	*F*	*p*
Lake	66	275 380	4 172.4	5.61	<0.0001
Sediment stratum	1	126 634.4	126 634.4	170.28	<0.0001
Replicate cores	1	979.6	979.6	1.3173	0.2544
Lake:depth	65	190 034.6	2 923.6	3.931	<0.0001
Residuals	82	60 979.6	743.7		

Note: Lake represents the variation among study lakes, sediment stratum represents the variation between present-day and preindustrial sediment, and replicate cores represents the variation in sediment Hg concentrations among separate cores at the same depth.

minimized by considering profundal sediments alone (Landers et al. 1998). Nonstandardized Hg concentrations were examined for differences between bedrock classes (i.e., on and off the Precambrian Shield) and time period (i.e., preindustrial and present day). A two-way ANOVA indicated a significant interaction in Hg concentrations between bedrock class and time period ($F_{[1,343]} = 15.58$, $p = 0.0001$). Therefore, separate one-way ANOVAs were conducted for lakes on and off the Precambrian Shield. Surface sediments had significantly higher Hg_{total} concentrations on Precambrian Shield bedrock ($F_{[1,170]} = 34.48$, $p < 0.0001$) than on calcareous bedrock. Preindustrial, Precambrian Shield sediments also had higher Hg_{total} concentrations than sediments of lakes off the Shield, but the relative difference was lower than for present-day sediments ($F_{[1,173]} = 4.51$, $p = 0.035$). Our results support previous findings (Friske and Coker 1995) that mean Hg concentration in present-day and preindustrial sediments is dependent, at least in part, on geology.

Sediment chronology (i.e., present-day and preindustrial sediment) was verified for a subset of our study lakes spanning a diverse geology using ^{210}Pb dating. The sampled cores were divided into eight regions (Table 3) and the mean ± SD age of present-day sediments (0.5–1 cm) and preindustrial sediments (30–35 cm) was inferred. The inferred age of present-day sediments was 3.4 ± 2.7 years across 30 sediment cores, while the inferred age at 30–31 cm was greater than 150 years with one exception. On average, the preindustrial era (1850) was inferred to lie at a depth of 19.3 ± 6.2 cm ($n = 30$, eight regions) below the sediment–water interface, supporting prior observations that 30+ cm captures pre-20th century horizons (Evans 1986; Dixit et al. 2002; Quinlan et al. 2003). Mean sedimentation rate was also determined from ^{210}Pb cores for the present and preindustrial eras. The mean sedimentation rate over the last 50 years averaged from eight lakes was 0.0154 ± 0.0017 g·cm^{-2}·year^{-1} and during the preindustrial era for intensively studied lakes in central Ontario was 0.0109 ± 0.0013 g·cm^{-2}·year^{-1} (Table 4).

Mercury concentrations were significantly correlated with organic matter content in surface ($r_s = 0.31$, $p < 0.0001$) and preindustrial sediments ($r_s = 0.29$, $p = 0.003$) according to Spearman rank correlation. Therefore, patterns of Hg concentrations were explored after standardizing for organic matter content. As found in unstandardized data, present-day sediments have significantly higher Hg on the Shield ($F_{[1,345]} = 10.60$, $p = 0.0015$) than off the Shield. However, following standardization, the difference in Hg content of preindustrial sediments between geological classes was no longer significant ($F_{[1,220]} = 0.317$, $p = 0.575$) (Table 5). These results suggest that the Hg content per unit of organic carbon was similar on and off the Shield in preindustrial times, but the Hg content per unit of organic carbon in Shield lakes has increased during the industrial period relative to non-Shield lakes. This difference might arise from changes to Hg input in Shield lakes or to changes in the decomposition of organic matter relative to the release of Hg in aquatic ecosystems on the Precambrian Shield.

Mercury concentrations in present-day sediments showed a weak but significant correlation with preindustrial Hg concentrations ($r_s = 0.222$, $p = 0.003$, $n = 172$) (Fig. 2). However, this correlation was no longer significant once Hg concentrations were standardized for organic matter content ($r_s = 0.105$, $p = 0.275$). This result suggests that part of the change in the Hg content of present-day sediments is due to changes in the ratio of Hg to organic matter.

An index that portrays the post-industrial increase in Hg concentrations is the sediment Hg enrichment factor (EF = $[Hg]_{present\ day}/[Hg]_{historical}$). The sediment Hg enrichment factor approximates the ratio of present-day to preindustrial fluxes to sediments, if we assume that sedimentation rate has remained constant through time. The EF was unaffected by the placement of sites on or off the Precambrian Shield (on the Shield: 0.6–4.8 (5th–95th percentiles), median = 2.3, $n = 135$; off the Shield: 0.5–5.1, median = 2.0, $n = 67$) ($p = 0.213$).

Semivariance increased with geographical distance in standardized, present-day Hg concentrations standardized by organic matter content ($Hg_{om\ corr}$), a phenomenon that was not observed in preindustrial sediments (Fig. 3) or in the organic matter content of lake sediments. This suggests that either the sources of Hg or the processes affecting the export, retention, sedimentation, or evasion of Hg from catchments have changed in a spatially dependent manner over the last century. The lack of spatial structure in preindustrial $Hg_{om\ corr}$ concentrations indicates that either the spatial structure is larger than the bounds of our analyses or the variance between lakes did not change as a function of distance.

By examining the drainage ratios of the study lakes, we can infer whether the watershed retention of Hg has changed since preindustrial times (Swain et al. 1992; Engstrom and Swain 1997). The drainage ratio explained a small but significant portion of preindustrial Hg concentrations in sediments ($R^2 = 0.108$, $F_{[1,86]} = 8.01$, $p = 0.006$). There was no improvement to this model when samples were separated based on their location on and off the Precambrian Shield. However, when we included water load (expressed as MAR

Table 3. Average age and standard deviation in years of sediment collected within the surficial (0.5–1 cm) and deep-core (30–31 cm) stratums inferred from ^{210}Pb dating.

Region	No. of lakes	Mean (SD) age (0–1 cm)	Age (30–31 cm)	Mean (SD) depth at 1850 cm
Dorset A lake	6	3.7 (1.6)	All >150	17.7 (2.8)
Lake of the Woods	2	2.5 (1.6)	All >150	23.5 (6.4)
Southeastern Ontario	4	3.0 (1.8)	>150, one at 1935	24.0 (12.1)
Muskoka	5	1.4 (0.4)	All >150	20.0 (3.0)
Bruce Peninsula	3	1.6 (2.8)	All >150	18.0 (7.0)
Manitoulin Island	1	1.0 (—)	All >150	26.0 (—)
Sudbury	4	5.6 (3.6)	All >150	11.5 (3.1)
Wawa	5	5.8 (4.1)	All >150	20.8 (2.4)
Overall	30	3.4 (2.7)		19.3 (6.2)

Table 4. Sedimentation rates (mean ± SD) inferred from ^{210}Pb dating in the last 50 years and in the preindustrial era from eight lakes within the study area.

		Mean sedimentation rate				
Lake	Region	Last 50 years ($g \cdot cm^{-2} \cdot year^{-1}$)	n	1850–1900 ($g \cdot cm^{-2} \cdot year^{-1}$)	n	Absolute difference in deposition
Crimson	South-central Ontario	0.0082±0.0006	7	0.0043±0.0011	2	0.0039
Dickie	South-central Ontario	0.0227±0.0017	10	0.0071±0.0010	2	0.0156
Harp	South-central Ontario	0.0202±0.0037	33	0.0076±0.0013	9	0.0126
Plastic	South-central Ontario	0.0097±0.0007	25	0.0197±0.0016	31	–0.0100
Red Chalk Main	South-central Ontario	0.0134±0.0021	37	0.0062±0.0012	11	0.0072
Heney	South-central Ontario	0.0124±0.0014	31	0.0044±0.0014	9	0.0080
Bigstone Bay	Northwestern Ontario	0.0188±0.0022	11	0.0208±0.0016	2	–0.0020
PP-1	Northwestern Ontario	0.0176±0.0015	36	0.0172±0.0010	3	0.0004
Overall		0.0154±0.0017		0.0109±0.0013		0.0040

Note: n represents the number of cores dated at each stratum within the study lakes.

Table 5. Mercury concentrations (mean ± SD) expressed as dry weight sediment extracted from surficial (0.5–1 cm) and deep-core (>30 cm) sediment within lakes upon granitic and limestone deposits.

		Hg ($ng \cdot g^{-1}$ dry weight)	
Location	Sediment	Within region	Within strata
On Shield	Surficial	176±5	241±7
	Deep core		111±7[a]
Off Shield	Surficial	144±7	189±10
	Deep core		99±10[a]

Note: Errors represent 1 SD from the mean concentration.
[a]Values are not significantly different from each other at the 95% confidence level.

(millimetres per year)) in the model, the variance explained was significantly improved for preindustrial sediments (R^2 = 0.313, $F_{[2,51]}$ = 12.28, $p < 0.0001$) (Fig. 4*a*). Conversely, a model including drainage ratio and MAR failed to explain a significant proportion of the variability in Hg concentrations in present-day sediments (Fig. 4*c*).

Spatial analyses indicated an increase in variance of Hg concentrations with distance between lakes (Fig. 3), so the above models were corrected using a cubic polynomial of x and y coordinates (Figs. 4*b* and 4*d*). The prediction of Hg concentrations in preindustrial sediments did not improve dramatically after accounting for spatial autocorrelation (Fig. 4*b*). This was expected given that variance in preindustrial Hg concentrations did not exhibit a strong trend with distance between lakes. Present-day Hg concentrations, however, displayed a tendency for higher variance with increasing geographic distance (Fig. 3), and model fit was much improved after adjusting for spatial structure (R^2 = 0.472, $F_{[1,60]}$ = 59.05, $p < 0.0001$) (Fig. 4*d*). Drainage ratio, however, remained unrelated to Hg concentrations in present-day sediments after correcting for spatial variance and MAR (partial t = 0.665, p = 0.508). Furthermore, although MAR was also spatially correlated (data not shown), results from a partial regression analysis indicate that MAR and A_d/A_o only shared 8% of explained variance with a cubic polynomial for the prediction of preindustrial $Hg_{sed\ core}$ and <1% in the prediction of present-day $Hg_{sed\ core}$. No spatial correlation was observed for A_d/A_o.

The Hg EF represents the relative increase resulting from anthropogenic activity. Presuming that sedimentation rates have not changed substantially, EF should account for variability in factors that influence the export rate of Hg among basins (e.g., surficial geology, depth of till, vegetation, and slope of watershed). However, since the preindustrial era, external factors such as sulfate deposition and subsequent catchment acidification may also have altered Hg export

Fig. 2. Total Hg concentrations in near-surface present-day (0.5–1 cm depth) versus deep preindustrial (>30 cm) sediment of lakes in south-central and eastern Ontario. The broken line represents a one-to-one relationship.

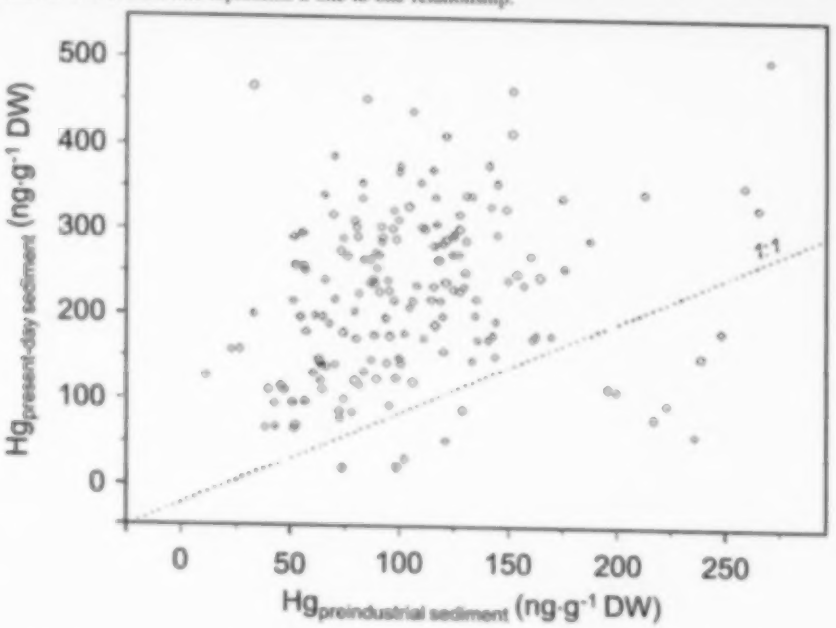
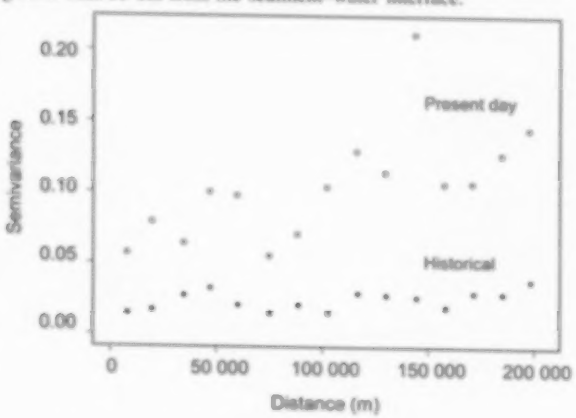


Fig. 3. Semivariogram of Hg concentrations in historical (●) and present-day (○) sediments as a function of distance. Semivariance was calculated using the GSTAT extension in S-Plus. The plot assumes a symmetrical change in variance with distance from the prediction point. Present-day sediments were collected at a depth of 0.5 to 1 cm and historical sediments were collected at depths greater than 35 cm from the sediment–water interface.



from lake watersheds (Miller and Akagi 1979; Hurley et al. 1995) and its accumulation in lake sediments (Vaidya and Howell 2002). Catchment acidification may have other indirect effects, such as lowering of DOC export (Ravichandran 2004; Wu et al. 2005), which could lead to reduced organic complexation and lower storage (Driscoll et al. 1995) as well as higher Hg volatilization (Ravichandran 2004). Studies have suggested that in drainage lakes, DOC may buffer the response to depositional changes by increasing the residence time of Hg in the water column (Watras et al. 1995). However, DOC concentrations in the study lakes were unable to explain any additional variability between drainage ratio and EF between the two time periods.

In contrast with the steady-state model used to predict preindustrial $Hg_{sed\ conc}$, MAR did not contribute to the explained variance in EF and was removed from the model. However, adjusting the EF model for lake pH increased the amount of explained variance ($F_{[2,48]} = 10.39$, $p < 0.001$), as did sulfate concentrations. EF did not increase in a linear fashion with drainage ratio, suggesting a deviation from steady-state conditions. Rather, an inverse relationship was observed and subsequently modelled (Table 6).

The impacts of anthropogenic acidification on lake pH varies on and off the Precambrian Shield. Monitoring data indicated that lakes located on the Shield had significantly lower pH than lakes off the Shield ($H = 21.915$, $p < 0.001$). However, pH values inferred from diatom assemblages preserved in lake sediments (Hall and Smol 1996; Reavie and Smol 2001) suggest that this was not the case in preindustrial times. A reanalysis of their findings indicates that the difference in preindustrial pH for lakes on and off the Shield was not significantly different ($t = 1.420$, $p = 0.171$), with a mean decline in pH of 0.51 and 0.29 since preindustrial times for lakes on granitic bedrock and calcareous limestone, respectively. Conversely, present-day lake pH inferred from sediment fossils (i.e., diatoms) is significantly different between lakes on and off the Shield (Holm–Sidak multiple comparison test: $t = 2.522$ $p = 0.020$). Similar patterns across regions, and through time, were observed for Hg concentrations (Table 2). After removing the variance explained by A_d/A_o and sulfate, the partial residuals in Hg concentration declined at pH values > 8.3 (Fig. 5).

Fig. 4. Observed and predicted Hg concentrations in (*a* and *b*) historical (>30 cm depth) and (*c* and *d*) present-day (0.5–1 cm) sediments of 54 headwater lakes standardized for organic matter content. Standardized Hg concentrations were predicted (*a* and *c*) before and (*b* and *d*) after correcting for autocorrelation using a cubic regression model, where *x* = latitude and *y* = longitude. $Hg_{historical} = 0.011 \pm 0.002(A_d/A_o) + 0.0008 \pm 0.0003(MAR)$; $Hg_{present\ day} = 0.0029 \pm 0.0043(A_d/A_o) + 0.0005 \pm 0.0006(MAR)$.

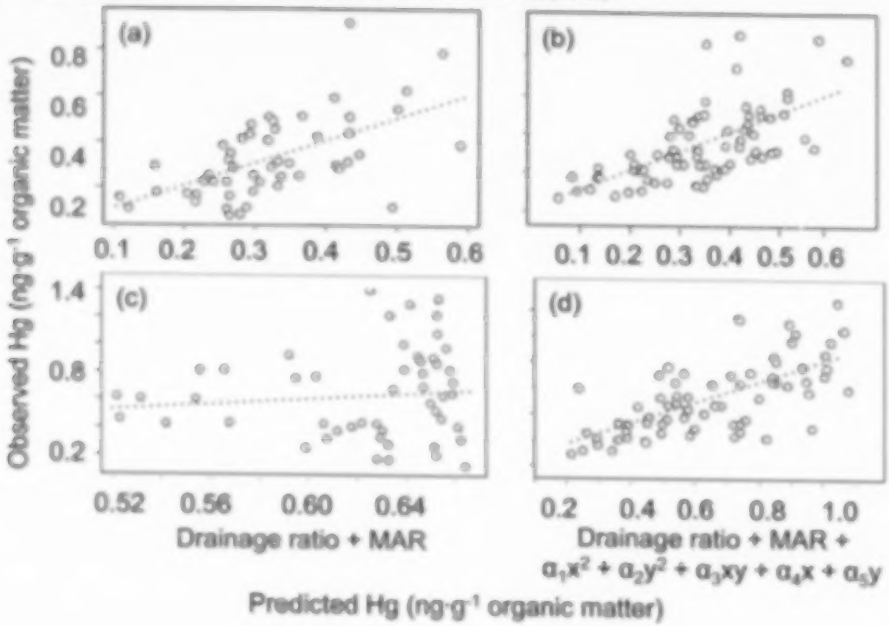


Table 6. Coefficients and the significance of the partial fit of each parameter in the prediction of Hg enrichment ($[Hg_{total}]_{present\ day}/[Hg_{total}]_{historical}$).

Parameter	Value	SE	*t*	*p*
Intercept	3.26	0.43	7.52	<0.0001
A_d/A_o^2	15.96	6.53	2.44	0.020
$n \times pH_{<8.3}$	–3.55	0.89	–4.01	<0.001
$n \times SO_4^{2-}$	–0.07	0.04	–1.68	0.1030

Note: pH was fit using a piecewise linear regression where the break point was determined by best fit. The break point was established at pH 8.3.

Finally, after removing the variance attributable to lake pH and sulfate concentration, we found that EF was strongly dependent on drainage ratio (Fig. 6). An inverse first-order polynomial was the model most suited to describe the partial fit of EF (Table 7). A downward curvilinear trend is expected only if the relative importance of terrestrial export was larger in the past than it is presently. Mercury enrichment appeared to reach a lower limit for drainage ratios >10 (adjusted $R^2 = 0.458$, $F_{[3,31]} = 9.282$, $p = 0.0001$).

Discussion

The primary objective of our study was to determine whether watersheds are at steady state with respect to Hg inputs and outputs. We hypothesized that if sedimentary Hg concentrations are a reflection of surface water concentrations, and if the net Hg export per area was independent of watershed size, Hg concentrations would display a consistent, linear increase with drainage ratio. Despite possible effects from sediment dilution, which may lower concentrations in lakes surrounded by larger watersheds, a significant linear relationship was found between A_d/A_o and Hg (nanograms per milligram of organic matter) in preindustrial sediments prior to adjusting for MAR. A recent study of a seepage lake and a drainage lake ($A_d/A_o = 2$) suggested that as fluvial loading increases, more Hg is lost from the water column through sedimentation (Watras and Morrison 2008). Watras and Morrison (2008) also found that fluvial inputs were lost more rapidly than direct pluvial inputs. While the increase in suspended matter from fluvial inputs likely increased sedimentation in drainage lakes, A_d/A_o remained the most important predictor of Hg (nanograms per milligram of organic matter) after adjusting for MAR.

The prediction of Hg concentrations in preindustrial sediments using drainage ratio was significantly improved by accounting for differences in MAR among watersheds, suggesting that sites with higher runoff may experience more erosion or may indicate basins that are more water saturated (i.e., anoxic conditions). The relationship between runoff and Hg export is well established (Allan et al. 2001; Shanley et al. 2005). For example, Shanley et al. (2005) found that stream discharge was the best predictor of Hg export, accounting for 20% of the variance, including interaction with other variables. This estimate is similar to that found in this study, where MAR explained 20% of variance in preindustrial Hg sediment concentration excluding drainage ratio. An increase in MAR would increase the lateral flow and should limit the adhesion of Hg to mineral soils (Watras

Fig. 5. Partial residuals in Hg enrichment from deep-core (>35 cm depth) to near-surface sediments (0.5–1 cm) in 54 headwater lakes as a function of pH after removing the variance attributable to drainage ratio and sulfate concentrations. Hg EF = $(A_d/A_w)^{-15.96} - 0.07(SO_4^{2-}) - (3.55(pH_{>8.3}))$.

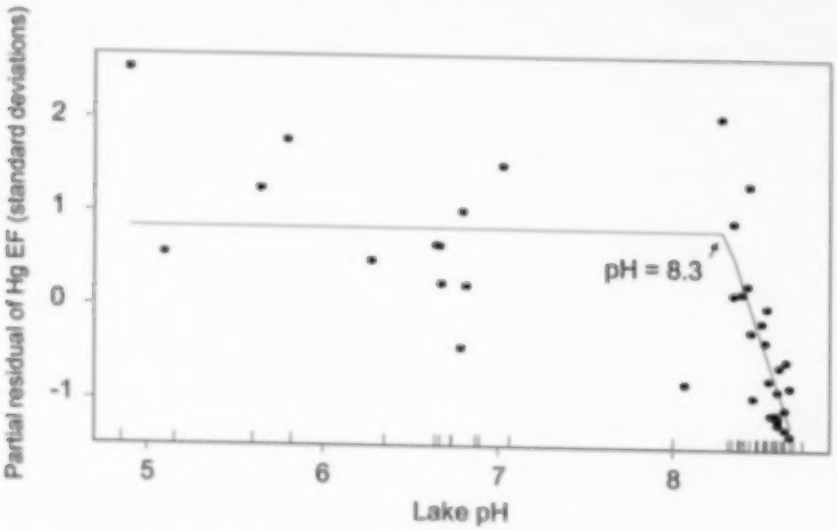


Fig. 6. Increase in Hg concentration from deep-core (>30 cm depth) to surface sediments (0.5–1 cm) in 54 headwater lakes of south-central Ontario presented before (○) and after (●) correcting for both pH and sulfate concentration as a function of drainage ratio. Hg EF = $(A_d/A_w)^{-15.96} - 0.07(SO_4^{2-}) - (3.55(pH_{>8.3}))$. The mean increase in Hg concentration over the study area is 2.46 ± 1.64 (broken line).

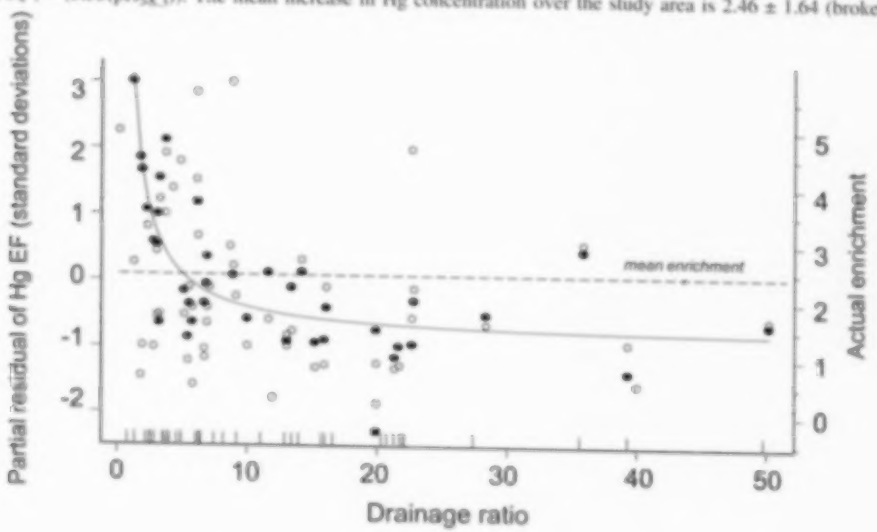


Table 7. Residual sum of squares and degrees of freedom for several models in the prediction of Hg enrichment ($[Hg_{total}]_{present\ day}/[Hg_{total}]_{bkgd\ recall}$).

Model	df	RSS
Drainage ratio	48	68.45
Drainage ratio + pH	46	47.16
Drainage ratio (polynomial) + pH + SO_4^{2-}	33	17.28
Drainage ratio (logarithmic) + pH + SO_4^{2-}	33	16.99

and Morrison 2008). Other studies have suggested that Hg fluxes to preindustrial sediments are largely controlled by watershed morphometry (Lindqvist et al. 1991; Swain et al. 1992; Meili et al. 2003) and surrounding geological deposits (Friske and Coker 1995; Landers et al. 1998), although we found no difference in Hg concentrations between lakes situated on or off the Precambrian Shield in this time period.

Mercury concentrations in present-day sediments showed no relationship with drainage ratio, suggesting that watersheds are presently not in steady state with respect to Hg deposition and export. In part, this may be because Hg con-

centrations in surficial sediments have been affected by anthropogenic disturbances that have altered Hg export from watersheds (e.g., acid deposition). For example, Hg concentrations displayed a different relationship with measured lake acidity above and below pH 8.3. Inorganic Hg may form oxyhydroxides at high pH (Lodenius and Autio 1989), and HgOOH may display a high affinity for charged particulate matter in soil, thus increasing the likelihood that it will be retained in the catchment at pH > 8 (Miller and Akagi 1979). In contrast, Hg-loaded complexes may be leached from the soil under acidic conditions; these complexes are primarily coloured substances (Mierle and Ingram 1991). In addition to reduced export, volatile species of Hg are formed at high pH, which has in some studies proven to be as high as 14% of that directly deposited from the atmosphere under ambient conditions (Vandal et al. 1991) and 45% with experimental additions (Southworth et al. 2007).

Despite the lack of relationship with present-day sediment Hg concentrations, drainage ratio exhibited a strong relationship with EF. Mercury enrichment was highest in watersheds with low drainage ratios and reached a plateau as catchment areas increased in proportion to lake area. Following the removal of the variance in Hg concentrations that could be explained by pH and sulfate, the form of the relationship between A_d/A_o and Hg enrichment was determined. The increased Hg enrichment at low drainage ratios could only be established if the proportion of Hg entering lakes from terrestrial sources was larger in the past than at present. Thus, our results suggest that more Hg is being retained within watersheds presently than in the past (i.e., large pools of Hg are being accumulated in catchments). The lack of relationship between Hg concentrations and drainage ratio in the present era may indicate that watershed systems are achieving a new steady state between terrestrial runoff and atmospheric deposition. Several other studies have reported that present-day watershed export remains elevated in comparison with observed changes in atmospheric deposition (Kamman and Engstrom 2002; Meili et al. 2003; Perry et al. 2005). As suggested in our study, Perry et al. (2005) implied that watershed Hg supplies to the lake are in excess of modern wet plus dry Hg deposition and speculated that the timing of watershed export to atmospheric declines may be controlled by watershed as well as lake storage.

We expect that lakes with proportionally smaller catchments will reach steady state at a faster rate than those with larger catchments. Our results suggest that lakes with low A_d/A_o ratios are responding to immediate changes in atmospheric deposition. The adsorption of Hg by soil particles may have sufficiently slowed the migration of Hg through catchments, thus delaying the full effect of anthropogenic activity on Hg in Ontario's surface waters to future decades. Mercury in preindustrial sediments was found to be largely correlated with the drainage ratios of watersheds in Ontario. The increase in Hg concentration with drainage ratio was similar among watersheds regardless of variance in other factors. This analysis indicates that during the preindustrial era, the proportion of Hg entering lake sediments from terrestrial versus atmospheric sources was similar among lakes. However, when we examined the enrichment of Hg from preindustrial to present-day sediments, we observed a nonlinear, inverse correlation with drainage ratio. The decrease in Hg enrichment as a function of drainage ratio supports the concept that Hg flux in watersheds is not at steady state with respect to deposition

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Fishing through (and up) Alaskan food webs

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Abstract: We used a 112-year time series of Alaskan fishery catches to test competing hypotheses concerning trends in mean catch trophic level, a widely used indicator of fisheries sustainability. We found that mean trophic level has generally remained steady or increased in recent decades on Alaska-wide and regional scales, indicating stable catches of high trophic level taxa. During historical periods of declining mean trophic level, catches of upper trophic level taxa either increased or remained steady, contrary to the predictions of the "fishing down the food web" hypothesis. Further, a climate index was highly correlated (r = 0.69–0.97) with mean trophic level and (or) the related fisheries in balance (FIB) index across climate regime shifts in the 1940s and 1970s, indicating that climate effects, particularly on high trophic level taxa, can act as the major driver of variability in these parameters. These results provide a contrast to the view of ubiquitous declines in mean trophic level of fishery catches, driven by overexploitation and serial stock replacement.

Résumé : Une série chronologique de 112 années de captures de pêches commerciales de l'Alaska nous a servi à comparer des hypothèses de rechange concernant les tendances dans le niveau trophique moyen des captures, un indicateur très utilisé de la durabilité des pêches. Le niveau trophique moyen s'est généralement maintenu stable ou a augmenté au cours des dernières décennies à l'échelle de l'Alaska tout entier et des régions, ce qui indique des captures stables des taxons de niveau trophique élevé. Durant les périodes passées de déclin du niveau trophique moyen, les captures des taxons de niveau trophique élevé ou bien ont augmenté ou alors sont restées stables, contrairement aux prédictions de l'hypothèse de « la pêche dans les niveaux inférieurs du réseau alimentaire ». De plus, il y a une forte corrélation (r = 0,69–0,97) entre un indice climatique et le niveau trophique moyen et (ou) l'indice apparenté FIB (« fisheries in balance », pêches en équilibre) au cours des changements de régime climatique des années 1940 et 1970, ce qui indique que les effets du climat, particulièrement sur les taxons de haut niveau trophique, peuvent agir comme facteurs explicatifs majeurs de la variabilité de ces paramètres. Nos résultats fournissent un contre-exemple à la perception qu'il existe à grande échelle des déclins dans les niveaux trophiques moyens des captures de pêche, dus à la surexploitation et le remplacement en série des stocks.

[Traduit par la Rédaction]

Introduction

The "fishing down the food web" hypothesis holds that declines in the mean trophic level of fishery catches are the result of the serial depletion of stocks, beginning with more valuable high trophic level species and proceeding to progressively lower trophic level, less valuable species (Pauly et al. 1998). This pattern of declining mean trophic level has been presented as ubiquitous (Pauly and Palomares 2005; Pauly and Watson 2005), and a series of influential papers has established the "fishing down" hypothesis as the dominant perspective from which to understand unsustainable fishery practices (Pauly et al. 1998, 2002, 2005). However, recent analysis has shown that fishing down the food web is specifically a feature of North Atlantic fisheries and that declining mean catch trophic levels in most other areas are produced by increasing exploitation of lower trophic levels, even as upper trophic level catches remain constant or increase (Essington et al. 2006). This pattern of sequential addition of progressively lower trophic level stocks to fisheries has been termed "fishing through the food web" (Essington et al. 2006). Because the idea of fishing down food webs has become so influential in the scientific literature, the "fishing through" hypothesis suggests the need for a widespread reassessment of trends in the mean trophic level of the catch in major fisheries, and the causes of those trends. An important part of establishing the fishing down the food web concept was the application of mean trophic level analysis to a variety of spatially disaggregated (i.e., national or regional) catch data sets with a wide range of underlying fishery types (Pauly et al. 2001, 2005). In a similar vein, simultaneously testing the "fishing through" and "fishing down" hypotheses with a variety of regional data sets will be an important step towards evaluating these two competing ideas.

In this paper, we use a 112-year commercial catch time

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series to elucidate trophic level trends in Alaskan fisheries. Alaskan ecosystems provide an interesting contrast to the Northwest Atlantic ecosystems that serve as the classic case of fishing down food webs, as catches of high trophic level groundfish have remained high in Alaska at the time when those fisheries have crashed in the North Atlantic. Furthermore, reorganization of marine communities following climate regime shifts is well recognized in Alaska (Anderson and Piatt 1999; Mantua and Hare 2002; Litzow and Ciannelli 2007), suggesting that climate change, rather than exploitation patterns, may at times be the dominant factor producing variability in fisheries productivity from Alaskan ecosystems. Our specific goals in this paper are (*i*) to explicitly test Alaskan fisheries for trends (increasing, decreasing, or variable) in mean trophic level and the related fisheries in balance (FIB) index of Pauly et al. (2000), (*ii*) to test predictions of the "fishing down" and "fishing through" hypotheses in situations where declines were observed in the mean trophic level, and (*iii*) to test for climate regulation of mean trophic level and FIB values during historical climate regime shifts, with specific attention to effects on high trophic level taxa, which are not accounted for in earlier attempts to make catch trophic level statistics robust to climate effects (Pauly and Watson 2005).

Materials and methods

Data sources

We used primary historical data sets to build a comprehensive catch history for Alaskan fisheries, including both landings and, when data were available, discards (Table 1). We began our time series in 1893, the first year for which salmon catch statistics were available. Catch data from early in the time series were often available only on a statewide basis and could not be assigned to a particular ecosystem. To provide the longest possible historical perspective on fisheries exploitation in Alaska, we aggregated all data into a statewide time series for analysis. However, spatial aggregation of data can obscure trends in mean trophic level (Pauly and Palomares 2005), so we also organized our data at the scale of the three large ecosystems that support Alaskan fisheries (Aleutian Islands, Bering Sea, and Gulf of Alaska). These ecosystem-specific time series began in the year when reliable spatially specific data could be acquired (1962 for the Aleutian Islands, 1954 for the Bering Sea, and 1956 for the Gulf of Alaska) (Livingston 2005). Data for the first two years of the Aleutian Islands time series show extremely small total catches (2×10^5 – 2×10^7 kg·year^{-1}), and we excluded these two years from analysis when fitting trend models to the time series, although FIB values for the region were calculated with 1962 as the reference year. All time series continued until 2004, the last year for which data were available, and almost all available data (>95% of total catch mass) were resolved to the species level (Table 1).

Most of the trophic level estimates that we used were derived from mass-balance models parameterized with extensive diet data (Aydin et al. 2007). The models used to derive these estimates took the microbial loop into account, which increases estimates by 0.5 levels compared with most other estimates. These trophic level estimates are specific to the Gulf of Alaska, Bering Sea, and Aleutian Islands, and when calculating mean values for the Alaska-wide time series, we used averages of the three values for widely exploited species and region-specific values for geographically restricted fisheries (Table 1). The trophic level of species not included in these models was estimated with values from FishBase (www.fishbase.org), adjusted upwards 0.5 levels to account for the microbial loop (Table 1).

During most of the 20th century, the Pacific Decadal Oscillation (PDO) index has captured the dominant mode of decadal-scale climate variability in Alaska (Bond et al. 2003), and sudden reorganizations of Alaskan marine communities following regime shifts in the PDO index are well recognized (Anderson and Piatt 1999; Mantua and Hare 2002; Litzow and Ciannelli 2007). The PDO index is the leading principal component of detrended (i.e., global warming trend removed) sea surface temperatures on a 5° × 5° grid in the North Pacific, poleward of 20°N (Mantua and Hare 2002). Winter PDO values most strongly capture the "regime" behavior of the index (Mantua and Hare 2002), and we used the November–March (calculated for the year corresponding to January) index mean as the measure of climate state in our study (data available at www.jisao.washington.edu/pdo/PDO.latest).

Analysis

We excluded marine mammal landings from our analysis because we were interested in elucidating trends in commercial fisheries as they are currently practiced (i.e., for fish and invertebrates). However, statewide time series with and without mammal landings were highly correlated for both mean trophic level ($r = 0.89$) and the FIB index ($r = 0.99$), suggesting that excluding mammal data did not materially change our results.

We calculated the mean trophic level of annual fishery catches with the formula

$$\text{(1)} \qquad \text{Mean TL}_k = \frac{\Sigma_i(\text{TL}_i \cdot Y_{ik})}{\Sigma_i Y_{ik}}$$

where TL_k is the trophic level in the year k, TL_i refers to the trophic level of the ith taxon, and Y_{ik} is the commercial catch of taxon i in year k.

The FIB index was developed in an attempt to distinguish "rational" switches to exploitation of lower trophic level taxa from switches caused by fishing down food webs (Pauly et al. 2000). The FIB index relates catches in a currency of primary production required (PPR) to support a fishery, estimated as

$$\text{(2)} \qquad \text{PPR} = C(1/\text{TE})^{\text{TL}}$$

where C is the size of the catch, TE is the transfer efficiency between trophic levels, and TL is the mean trophic level of the catch. Based on modeling of Alaskan marine food web dynamics (Aydin et al. 2007), we set TE = 0.1. The FIB index then measures change in PPR in a given year k from a baseline year 0 as

$$\text{(3)} \qquad \text{FIB}_k = \log(\text{PPR}_k) - \log(\text{PPR}_0)$$

To test for changes in trophic level and the FIB index through time, we used first-order (AR1) autoregressive error models, which correct regression estimates for autocorrela-

Table 1. Catch data sources for Alaskan commercial fisheries and estimated trophic level values used to compute mean trophic level of the catch.

Common name	Scientific name	Catch source[a]	Estimated trophic level	Trophic level source[b]
Sea cucumbers	Holothuroidea	1	2.0	1
Sea urchins	*Strongylocentrotus* spp.	1	2.0	1
Abalone	*Haliotis* spp.	1	2.5	1
Clams	Bivalvia	1, 3	2.5	1
Scallops	*Patinopecten, Chlamys*	1	2.5	1
Shrimp	Pandalid spp.	1, 2, 4	2.9	1
Snails	*Neptunea* spp., *Buccinum* spp.	1	2.9	1
Dungeness crab	*Cancer magister*	1, 2	3.1	1
Hair crab	*Erimacrus isenbeckii*	1	3.1	1
King crab	*Lithodes, Paralithodes*	1	3.4	1
Opilio crab	*Chionoecetes opilio*	1	3.4	1
Tanner crab	*Chionoecetes bairdi*	1	3.4	1
Alaska plaice	*Pleuronectes quadrituberculatus*	6	3.5	1
Pacific herring	*Clupea pallasii*	1, 2, 4, 7, 8	3.5	1
Smelt	Osmeridae	1, 2	3.5	1
Northern rockfish	*Sebastes polyspinis*	1, 6	3.6	1
Other flatfish	Pleuronectiformes	1, 2, 6	3.6	1
Pacific Ocean perch	*Sebastes alutus*	1, 6	3.6	1
Pacific tomcod	*Microgadus proximus*	1	3.6	1
Rock sole	*Lepidopsetta* sp.	6	3.6	1
Yellowfin sole	*Limanda aspera*	6	3.6	1
Sharpchin rockfish	*Sebastes zacentrus*	1, 6	3.6	1
Dusky Rockfish	*Sebastes ciliatus, S. variabilis*	1, 6	3.7	1
Atka mackerel	*Pleurogrammus monopterygius*	6	3.7	1
Chum salmon	*Oncorhynchus keta*	1, 5, 6	3.7	2
Sockeye salmon	*Oncorhynchus nerka*	1, 5, 6	3.7	2
Squid	Teuthoidea	1, 6	3.7	1
Walleye pollock	*Theragra chalcogramma*	2, 6	3.7	1
Other rockfish	*Sebastes* sp.	6	3.8	1
Octopus	*Octopus dofleini*	1, 6	3.8	1
Steelhead	*Oncorhynchus mykiss*	1, 2	3.8	1
Shortraker rockfish	*Sebastes borealis*	1, 6	3.9	1
Thornyheads	*Sebastolobus* sp.	1, 6	3.9	1
Rougheye rockfish	*Sebastes aleutianus*	1, 6	4.0	1
Salmon bycatch	*Oncorhynchus* sp.	6	4.0	2
Pacific cod	*Gadus macrocephalus*	1, 2, 6	4.1	1
Sablefish	*Anoplopoma fimbria*	1, 2, 6	4.1	1
Coho salmon	*Oncorhynchus kisutch*	1, 5, 6	4.2	2
Pink salmon	*Oncorhynchus gorbuscha*	1, 5, 6	4.2	2
Arrowtooth flounder	*Atheresthes stomias*	6	4.3	1
Lingcod	*Ophiodon elongatus*	1, 2	4.3	1
Spiny dogfish	*Squalus acanthias*	2, 6	4.3	1
Skates	Rajidae	1	4.4	1
Chinook salmon	*Oncorhynchus tshawytscha*	1, 5, 6	4.4	2
Greenland turbot	*Reinhardtius hippoglossoides*	6	4.6	1
Pacific halibut	*Hippoglossus stenolepis*	9, 10, 11	4.6	1
Other sharks	Elasmobranchii	2, 6	4.8	1

[a]Catch sources: 1, ADF&G Annual Management Reports, Fishticket database (1969+), Alaska Catch and Production Reports (1966–1985), Annual Reports (1949–1962), available at www.sf.adfg.state.ak.us/statewide/divreports/html/advSearch.cfm [accessed 12 August 2008]; 2, US Bureau of Fisheries: Report on the Salmon Fisheries of Alaska (1903–1905), The Fisheries in Alaska (1906–1910), Alaska Fishery and Fur Seal Industries (1911–1942), these reports from the US Bureau of Fisheries are available through the US archives and are referenced www.archives.gov/research/guide-fed-records/groups/022.html#22.4 [accessed 22 Oct. 2008]; 3, Nickerson 1975; 4, Forrester et al. 1983; 5, INPFC 1979, INPFC 1992; 6, North Pacific Fishery Management Council Stock Assessment and Fishery Evaluation Documents, www.fakr.noaa.gov/npfmc/SAFE/SAFE.htm [accessed 22 Oct. 2008]; 7, Skud et al. 1960; 8, Guttormsen et al. 1990; 9, Bell et al. 1952; 10, Myhre et al. 1977; 11, www.iphc.washington.edu/halcom/pubs/rara/IPHCRARA.htm, www.iphc.washington.edu/halcom/research/sa/legacy.data/landings.data/hist.comcat.txt [accessed 12 August 2008].

[b]Trophic level sources: 1, Aydin et al. 2007 (note that TL of king crab, Alaska Plaice, other flatfish, and Pacific halibut are estimated from Bering Sea and Gulf of Alaska data only; Atka mackerel are estimated from Aleutian Island data only; Pacific cod are estimated from Bering Sea data only; TL of chum salmon is set equal to that of sockeye salmon); 2, FishBase, http://filaman.ifm-geomar.de/search.php?lang=English [accessed 12 August 2008].

tion in time series data (Fuller 1978; SAS Institute, Inc. 2005). Competing linear, logarithmic, and quadratic AR1 models allowed us to explicitly test trophic level and FIB time series for monotonic change (increasing or decreasing), change followed by stability, and variable change through time, respectively. We compared models with Akaike's information criterion values adjusted for small sample size (AIC_c) (Burnham and Anderson 1998). We report ΔAIC_c values, which allow the relative support for competing models to be assessed, and we also report R^2 and p values for each selected model.

Following Essington et al. (2006), we used mean trophic level declines of 0.15 units or more for tests of the competing fishing down and fishing through hypotheses. We calculated the catch of upper trophic level and lower trophic level taxa during the period of decline (i.e., from the year of maximum mean trophic level to the year of minimum mean trophic level), using the mean trophic level of the total catch at the onset of the decline as the dividing point between the high and low trophic level groups. We then fit linear AR1 models to catch values for each group to test for significant changes over time. Although both hypotheses predict increases in lower trophic level groups during declines in mean trophic level of the catch, the fishing down hypothesis predicts simultaneous declines in upper trophic level taxa, whereas the fishing through hypothesis predicts stable or increasing upper trophic level catches.

Because we were specifically interested in testing for climate regime shift effects on mean trophic level and FIB values, we restricted our analysis of climate effects to span recognized regime shifts in the PDO index, which occurred in 1924–1925, 1946–1947, and 1976–1977 (Mantua and Hare 2002). Statewide commercial fisheries were judged to be too poorly developed prior to 1924–1925 to allow for a robust comparison across that regime shift, so statewide mean trophic level and FIB values were compared with the PDO index across the 1946–1947 regime shift, from 1924 until the last year of the preindustrial fishery era (1958, see Results). We analyzed the effects of the 1976–1977 regime shift on each ecosystem separately. For the Gulf of Alaska, PDO scores were compared with mean trophic level and FIB values for the years 1973 (when a large shrimp fishery matured) to 1990 (after the PDO had lost its autocorrelated "regime" behavior; Bond et al. 2003). We used the same period for analysis of Aleutian Island and Bering Sea fisheries for the sake of consistency. We smoothed the PDO index with a three-year running mean to account for high interannual variability that is imposed on decadal-scale signals in physical parameters (Hare and Mantua 2000), and we lagged PDO values two years to account for the observed lag of climate effects on Alaskan ecosystems (Litzow 2006). We corrected PDO–fisheries comparisons for temporal autocorrelation with the modified Chelton method (Pyper and Peterman 1998) and report these results with adjusted sample size (n') and probability values (p'). We log-transformed catch sizes to achieve approximate normality and set $\alpha = 0.05$ throughout.

Results

Fishery trends

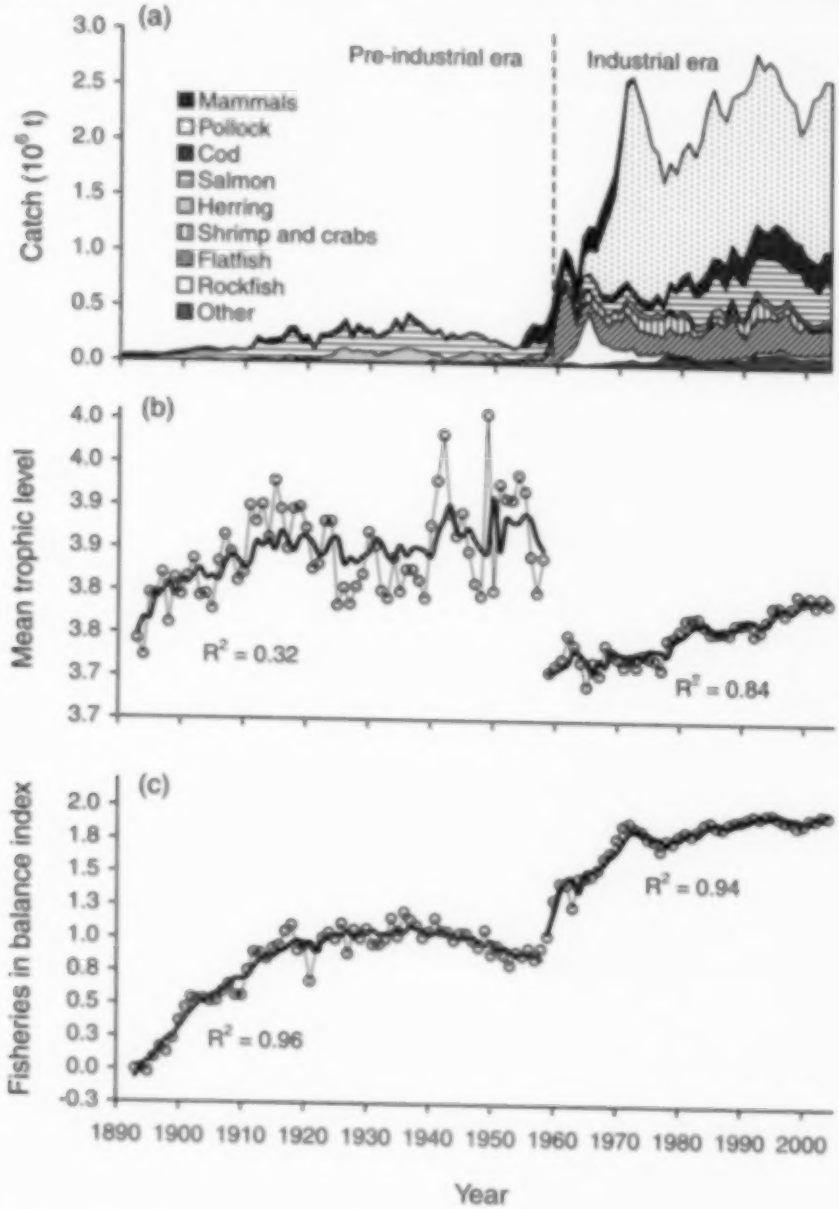
Alaskan catches fell into two distinct historical periods: the preindustrial era (1893–1958), when total catches peaked at 4.20×10^6 kg·year^{-1} and were dominated by salmon (*Oncyrynchus* spp.) and Pacific herring (*Clupea pallasii*), and the industrial era (1959 to present), when total catches peaked at 2.85×10^6 kg·year^{-1} and were dominated by walleye pollock (*Theragra chalcogramma*), with lesser contributions from Pacific cod (*Gadus macrocephalus*), salmon, crustaceans (crabs and Pandalid shrimp), flatfish (Pleuronectidae), and rockfish (*Sebastes* spp.) (Fig. 1*a*). Because of the different composition of the fishery during the two periods and the nearly order of magnitude difference in catch size, we analyzed statewide trends in mean trophic level and FIB values separately for the two periods. During the preindustrial era, trend in statewide mean trophic level was best explained by a logarithmic model ($R^2 = 0.32$, $p = 0.001$; Table 2), indicating an increasing trend followed by a period of high variability. At the onset of the industrial era, mean statewide trophic level fell precipitously (Fig. 1*b*) but then increased steadily through the following decades (linear best model, $R^2 = 0.84$, $p < 0.0001$; Table 2). Statewide FIB values were best described by a quadratic model during the preindustrial era, indicating a declining trend during the 1930s to 1950s ($R^2 = 0.96$, $p < 0.0001$; Table 2). Statewide FIB values increased dramatically at the onset of industrial era fisheries and then stabilized in recent decades (Fig. 1*c*), a pattern that was best described by a logarithmic model ($R^2 = 0.94$, $p < 0.0001$).

Regional-scale analysis shows that both mean trophic level (Fig. 2*a*) and FIB values (Fig. 2*b*) have declined in the Aleutian Islands in recent decades. These patterns resulted in the selection of quadratic models for both parameters (trophic level, $R^2 = 0.83$, $p < 0.0001$; FIB, $R^2 = 0.70$, $p < 0.0001$). Bering Sea fisheries were characterized by rapid increases in both mean trophic level and FIB values in the 1950s and 1960s and stable values in recent decades (Figs. 2*c*, 2*d*), best described by logarithmic models in both cases (trophic level, $R^2 = 0.78$, $p < 0.0001$; FIB, $R^2 = 0.96$, $p < 0.0001$; Table 2). Gulf of Alaska mean trophic level showed a strong declining trend (0.35 units) from 1954 until the early 1970s (Fig. 2*e*), best described by a linear model ($R^2 = 0.78$, $p < 0.0001$). Trophic level values rebounded rapidly (0.37 unit increase) following the 1976–1977 climate regime shift and then stabilized (Fig. 2*e*), a pattern best described by a quadratic model ($R^2 = 0.88$, $p < 0.0001$; Table 2). Gulf of Alaska FIB values showed high variability prior to the regime shift (Fig. 2*f*), a pattern poorly described by the best (logarithmic) model ($R^2 = 0.27$, $p = 0.77$; Table 2), but showed a strong (quadratic) increase following the regime shift ($R^2 = 0.81$, $p < 0.0001$).

Mechanisms underlying trends

We identified three instances in which mean trophic level declined at least 0.15 units: statewide 1949–1965 (0.32 units), Aleutian Islands 1973–1996 (0.15 units), and Gulf of Alaska 1956–1973 (0.35 units). A statewide drop of 0.19 units over 1942–1948, which coincided with World War II and was followed by an immediate recovery of 0.21 units in 1949, was treated as a short-term aberration rather than evidence of a trend and was not included in analysis. Upper trophic level catches increased in the statewide example ($R^2 = 0.85$, $p = 0.01$; Fig. 3*a*) and the Aleutian Islands

Fig. 1. Catch history of statewide Alaskan commercial fisheries, 1893–2004. (*a*) Composition of the catch, indicating division of time series into preindustrial (pre-1959) and industrial (1959 and later) eras. Marine mammal landings are illustrated for sake of comparison but were excluded from analysis. (*b*) Mean trophic level of the catch and (*c*) fisheries in balance index for the two periods. Trend lines (bold lines) in (*b*) and (*c*) are best first-order autoregressive error models selected from candidate linear, logarithmic, and quadratic models using Akaike's information criterion (AIC).



(R^2 = 0.38, p = 0.03; Fig. 3*b*) and showed no trend in the Gulf of Alaska (R^2 = 0.12, p = 0.14; Fig. 3*c*), supporting the predictions of the fishing through hypothesis and failing to support the fishing down hypothesis.

Our analysis of climate effects found several instances of strong coupling between the PDO index and fisheries. Statewide FIB values for 1924–1958 were strongly correlated with the PDO (r = 0.69, n' = 8.6, p' = 0.03; Fig. 4*a*), although mean trophic level values, which showed little trend through that period, were not (r = –0.18, n' = 17.0, p' = 0.48). During 1973–1990, Aleutian Island FIB values were correlated with the PDO index (r = 0.79, n' = 11.0, p' = 0.002; Fig. 4*b*), though mean trophic level values were not (r = 0.28, n' = 5.4, p' = 0.54). In the Gulf of Alaska dur-

Table 2. Best models (in descending order) for trends in mean trophic level (TL) and fisheries in balance (FIB) index for Alaskan commercial fishery catches on statewide and regional scales using Akaike's information criterion (AIC).

Response variable	Model[a]	AIC_c[b]	ΔAIC_c	R^2	p'
Statewide analysis[c]					
Preindustrial TL (1893–1958)	ln(Year)	−214.14	0.00	0.32	0.001
	Year	−210.82	3.32		
	Year × year^2	−209.76	4.38		
Preindustrial FIB (1893–1958)	Year × year^2	−134.59	0.00	0.96	<0.0001
	ln(Year)	−114.23	20.36		
	Year	−108.71	25.88		
Industrial TL (1959–2004)	Year	−272.74	0.00	0.84	<0.0001
	Year × year^2	−270.75	1.99		
	ln(Year)	−264.12	8.62		
Industrial FIB (1959–2004)	ln(Year)	−131.51	0.00	0.94	<0.0001
	Year × year^2	−115.26	16.25		
	Year	−107.57	23.94		
Regional analysis					
Aleutian Islands TL (1964–2004)	Year × year^2	−134.75	0.00	0.83	<0.0001
	ln(Year)	−132.56	2.19		
	Year	−129.91	4.84		
Aleutian Islands FIB (1964–2004)	Year × year^2	−38.57	0.00	0.70	<0.0001
	Year	−37.89	0.68		
	ln(Year)	−35.41	3.16		
Bering Sea TL (1954–2004)	ln(Year)	−280.68	0.00	0.78	<0.0001
	Year × year^2	−277.89	2.79		
	Year	−276.38	4.30		
Bering Sea FIB (1954–2004)	ln(Year)	−64.39	0.00	0.96	<0.0001
	Year	−58.60	5.79		
	Year × year^2	−44.64	19.75		
Gulf of Alaska TL[d] (1956–1976)	Year	−57.74	0.00	0.78	<0.0001
	ln(Year)	−54.55	3.19		
	Year × year^2	−54.30	3.44		
Gulf of Alaska TL (1977–2004)	Year × year^2	−106.13	0.00	0.88	<0.0001
	ln(Year)	−103.08	3.05		
	Year	−98.30	7.83		
Gulf of Alaska FIB (1956–1976)	ln(Year)	−29.90	0.00	0.27	0.77
	Year	−29.81	0.09		
	Year × year^2	−29.03	0.87		
Gulf of Alaska FIB (1977–2004)	Year × year^2	−66.59	0.00	0.81	<0.0001
	ln(Year)	−61.73	4.86		
	Year	−58.82	7.77		

[a] All models are first-order autoregressive (AR1) models: year, linear model; log(year), logarithmic model; year × year^2, quadratic model.

[b] AIC score corrected for small sample size.

[c] p values assume AR1 parameter as given.

[d] Gulf of Alaska analysis performed separately for periods before and after the 1976–1977 climate regime shift.

ing the same period, both FIB values ($r = 0.92$, $n' = 4.5$, $p' = 0.02$; Fig. 4c) and mean trophic level ($r = 0.97$, $n' = 4.6$, $p' = 0.004$; Fig. 4d) were highly correlated with the PDO index.

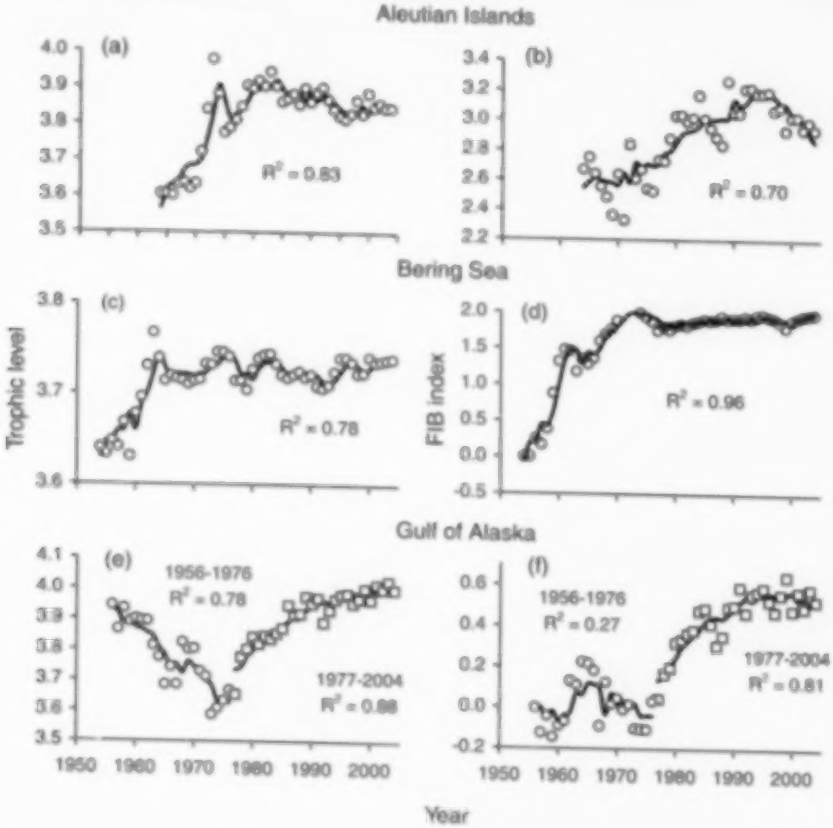
In the Bering Sea, neither FIB values ($r = 0.03$, $n' = 10.9$, $p' = 0.93$) nor mean trophic level ($r = -0.36$, $n' = 6.4$, $p' = 0.41$) were correlated with the PDO index.

The trophic level – PDO relationship in the Gulf of Alaska was largely the result of climate effects on the catch of higher trophic level taxa. Catches of taxa with trophic level greater than the 1973–1990 mean (3.81) were highly correlated with the PDO ($r = 0.93$, $n' = 4.8$, $p' = 0.01$), while we could not reject the null hypothesis of no relationship between the PDO and the catch of lower trophic level taxa ($r = 0.40$, $n' = 6.1$, $p' = 0.18$).

Discussion

A broad consensus holds that global fisheries are poorly managed and unsustainable (Hutchings 2000; Jackson et al. 2001; Pauly et al. 2002), and overexploitation of high trophic level stocks has been identified as a central part of this problem (Myers and Worm 2003). However, a rigorous debate has recently played out over the exact nature of the global fisheries crisis (e.g., Sibert et al. 2006; Worm et al.

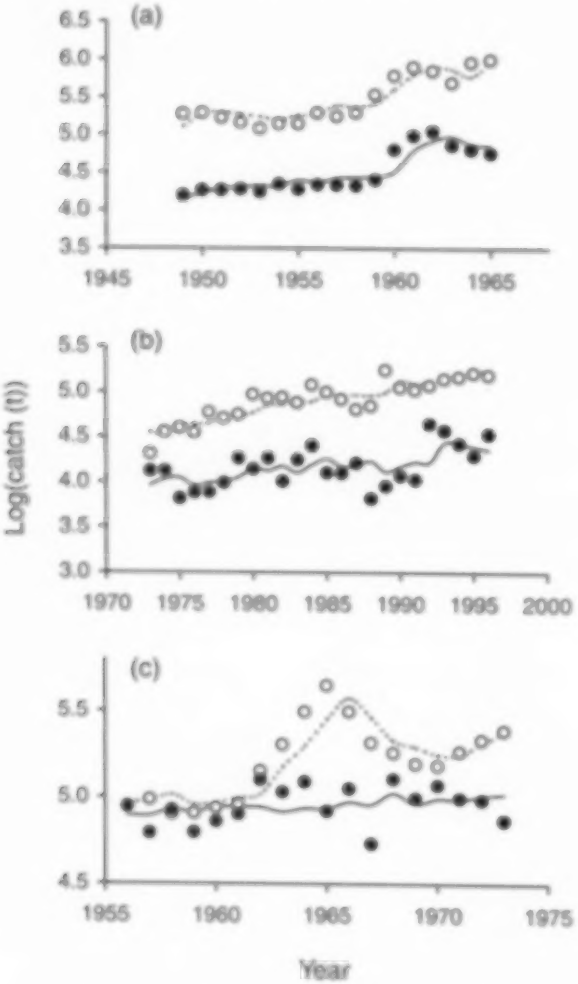
Fig. 2. Regional-scale analysis of time series in mean trophic level and fisheries in balance (FIB) index for commercial fishery catches in (*a*, *b*) Aleutian Islands, (*c*, *d*) Bering Sea, and (*e*, *f*) Gulf of Alaska. Trend lines indicate best first-order autoregressive error models selected from candidate linear, logarithmic, and quadratic models using Akaike's information criterion (AIC). Gulf of Alaska trends were calculated separately for periods before and after the 1976–1977 climate regime shift.



2006; Hilborn 2007). Explicit tests of proposed ecosystem-based fisheries metrics are required for the exact nature of management failures to be understood. To our knowledge, our study and the study of Essington et al. (2006) are the only two published studies to explicitly test for declining catches of upper trophic level taxa during instances of declining mean trophic level of fisheries catches, although de Mutsert et al. (2008) have also noted the sensitivity of the mean trophic level index to large catches of low trophic level taxa. Our results show that historical periods of declining mean trophic level in Alaskan commercial fishery catches were due to increases in lower trophic level catches (fishing through the food web), rather than declines in upper trophic level catches (fishing down the food web). Identifying examples of successful management is an important step for improving failed management approaches. On both regional and Alaska-wide spatial scales, we found that in recent decades the mean trophic level of the catch and FIB values have generally been stable, or actually increased. These results suggest that Alaskan fisheries have, on the whole, been generally well managed, and the Alaskan example may therefore provide an instructive example of sustainable industrial-scale exploitation.

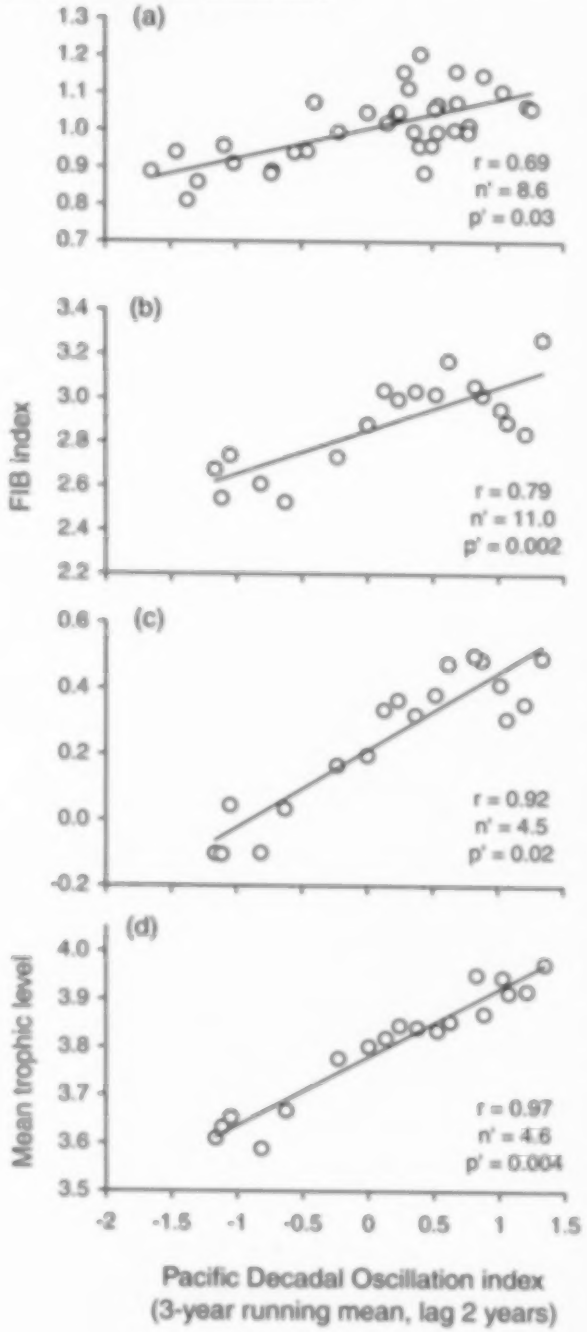
We found significant correlations between the PDO index and mean trophic level and (or) FIB values in the statewide analysis of the effects of the 1946–1947 regime shift and two of the three regional analyses of the 1976–1977 regime shift. However, Bering Sea mean trophic level and FIB values showed no correlation with the PDO index, even though the 1976–1977 regime shift had strong community-level impacts in that ecosystem (Conners et al. 2002; Hunt et al. 2002). Walleye pollock dominated Bering Sea catches during the period that we tested for climate effects (1973–1990) and made up a remarkably constant proportion of the total catch (85% in 1973, 73% in 1990). The mostly constant mean trophic level and FIB values in the Bering Sea during this period are therefore largely the result of sustained exploitation of this single species. Walleye pollock recruitment is believed to have been greatly enhanced by the 1976–1977 regime shift (Hunt et al. 2002), so the sustained massive exploitation of this species (average Bering Sea catch during 1970–2004 = 1.25×10^9 kg·year^{-1}) has likely been supported by climate effects. In any case, the differing results from these three neighboring ecosystems show how either climate change or fishing practices can be the primary drivers of variability in mean trophic level and

Fig. 3. Time series of log-transformed catches of upper (●) and lower (○) trophic levels during three periods of declining mean trophic level of Alaskan commercial fishery catches: (*a*) statewide catches for 1949–1965, (*b*) Aleutian Islands catches for 1973–1996, and (*c*) Gulf of Alaska catches for 1956–1973. Trend lines are first-order autoregressive linear models. Dividing point between upper and lower groups is mean trophic level of the catch during the first year plotted for each panel. Upper trophic level catches increased significantly during periods of declining mean trophic level statewide ($p = 0.01$) and in the Aleutian Islands ($p = 0.03$) and showed no significant trend ($p = 0.14$) in the Gulf of Alaska.



FIB values, which underlines the importance of simultaneously considering climate and fishing effects when attempting to understand the dynamics of exploited ecosystems. Attention to climate effects is particularly important for management of continental shelf ecosystems that are prone to sudden shifts between alternate steady states (Anderson and Piatt 1999; Chavez et al. 2003; Litzow and Ciannelli 2007), as a management approach based solely on the current ecosystem state can increase the chance of a sudden, ir-

Fig. 4. Climate effects on Alaskan fishery trends: (*a*) statewide fisheries in balance (FIB) index values for 1924–1958, (*b*) Aleutian Islands FIB for 1973–1990, (*c*) Gulf of Alaska FIB for 1973–1990, and (*d*) Gulf of Alaska mean trophic level for 1973–1990. Test periods for climate–fisheries comparisons span regime shifts in the Pacific Decadal Oscillation index. Values of n' and p' have been corrected for temporal autocorrelation.



reversible change to an alternate state (Scheffer et al. 2001; Peterson et al. 2003). Efforts to distinguish climate effects from fishery effects in evaluating trends in mean catch trophic level have consisted of excluding lower trophic level taxa from analysis (Pauly and Watson 2005). However, the very strong linkage between the PDO index and Gulf of Alaska mean trophic level during 1973–1990 was specifically the result of correlation between climate and catches of upper trophic level taxa ($r = 0.93$), not lower trophic level taxa ($r = 0.40$), which suggests the limitations of considering climate effects on lower trophic level catches only.

The rapid increase in the mean trophic level of Gulf of Alaska catches following the 1976–1977 regime shift reflects the collapse of low trophic level crustacean stocks and rapid growth in upper trophic level salmon and groundfish stocks. Catches of crustaceans were declining in many areas of the Gulf of Alaska before 1976–1977, indicating that stocks were overfished before the regime shift occurred (Orensanz et al. 1998). However, several lines of evidence lead us to conclude that climate change played an important role in changing the structure of Gulf of Alaska fisheries following 1976–1977 and that the PDO–fishery correlations that we found therefore reflect a causative relationship. First, the 1976–1977 regime shift resulted in simultaneous community reorganization in diverse ecosystems around the North Pacific, strongly suggesting climate forcing of ecological processes (Chavez et al. 2003). Second, a causative mechanism (changing trophic control) has been identified as linking this regime shift to ecological change in a Gulf of Alaska bay where crustacean stocks had previously been steady (Litzow and Ciannelli 2007). Whatever the relative contribution of climate change and overfishing as causative mechanisms, the rapid increase in mean trophic level following the regime shift is an example of stock collapse leading to increasing, rather than decreasing, mean trophic level of the catch (i.e., fishing up the food web), which contrasts with the better-known North Atlantic example (Essington et al. 2006), and further argues against the hypothesis that declining mean trophic levels are an inevitable result of stock collapse (Pauly and Watson 2005). The total commercial catch in the Aleutian Islands increased rapidly during 1973–1990, as reflected in increasing FIB values during this time. Our analysis does not allow us to rule out the alternate hypothesis that PDO–FIB correlations in the Aleutian Islands were due to coincidental fisheries expansion, rather than climate effects. However, modeling of the Aleutian Islands ecosystem does suggest that the PDO may have strong population-level effects on commercially important fish species (Guénette et al. 2006; North Pacific Fishery Management Council 2007), supporting the idea that climate was an important driver of the correlation that we found. Given the strong potential for contemporary climate change to reorganize ecosystems supporting fisheries in Alaska (Grebmeier et al. 2006; Mueter and Litzow 2008) and globally (Walther et al. 2002), understanding the interaction of climate change and fisheries effects on ecosystems is an important research goal. A better approach for distinguishing climate-generated and fishery-generated effects on the mean trophic level of the catch will be needed if the mean trophic level metric is to be useful in this context.

If serial stock depletion was not the cause of the three instances of declining mean trophic level of the catch that we document, what other factors, besides regime shift effects, were at work? The statewide decline in trophic level during 1949–1965 was an obvious case of stock addition, specifically the massive exploitation of yellowfin sole (*Limanda aspera*) and Pacific ocean perch (*Sebastes alutus*) by foreign fleets at the onset of industrial fishing (reflected in the "flatfish" and "rockfish" categories herein). These species feed at a lower trophic level than the salmon species that had previously dominated the statewide catch. The decline in Gulf of Alaska mean trophic level during 1956–1973 was also a case of stock addition, with massive increases in Pacific ocean perch catches and steady growth in fisheries for crustaceans (red king crab (*Paralithodes camtschaticus*), tanner crab (*Chionoecetes bairdi*), and Pandalid shrimp) set against a background of fairly constant salmon catches.

The decline in Aleutian Island mean trophic level during 1973–1996 was also driven by stock addition, in this case by increasing catches of walleye pollock and Atka mackerel (*Pleurogrammus monopterygius*), which brought the mean trophic level down from the 1973 peak value of 4.0 units. Mean trophic level was further reduced by the increase in Pacific ocean perch catches after this stock recovered and catches increased in the 1990s. Declines in mean trophic level were also brought about by changes within the upper trophic level complex, as catches of Greenland turbot (*Reinhardtius hippoglossoides*, trophic level = 4.6) and arrowtooth flounder (*Atheresthes stomias*, trophic level = 4.3) declined and catches of Pacific cod (*Gadus macrocephalus*, trophic level = 4.2) increased. These changes within the higher trophic level group might be construed as evidence of fishing down the food web. However, declines in Greenland turbot catches in the late 1970s occurred when the foreign fishery was phased out, and continued reductions in catch through the 1990s were management restrictions in response to declining recruitment (North Pacific Fishery Management Council 2007). Arrowtooth flounder catches in the 1970s were mostly bycatch from Greenland turbot fisheries and also declined with the cessation of foreign fishing. Arrowtooth flounder in the Aleutian Islands have been lightly exploited since the 1970s, mostly as bycatch in other fisheries, and the stock is believed to have increased fivefold during the last three decades (North Pacific Fishery Management Council 2007). Models suggest that Pacific cod recruitment in the region has also increased approximately fivefold following the 1976–1977 regime shift, explaining the increased harvest of that species (North Pacific Fishery Management Council 2007). Changes in exploitation within the high trophic level group are therefore apparently the result of conservation measures (Greenland turbot), market forces (arrowtooth flounder), and increases in abundance (Pacific cod). Catches of Aleutian Island taxa at trophic level 4.0 or higher increased 140% during 1973–1996, whereas catches of taxa at trophic levels below 4.0 increased 870% during the same period, a pattern that describes stock addition rather than stock depletion.

Finally, it is important to note that we are not claiming that all Alaskan fisheries have been, or are, properly managed. Commercial exploitation has doubtless had profound effects on Alaskan marine ecosystems (Jackson et al. 2001), and the complexity and diffuse linkages of marine food

webs make these effects extremely difficult to understand (e.g., Merrick et al. 1997; Springer et al. 2003). In particular, serial stock addition and increasing fishing capacity with the onset of industrial fishing in the 1950s produced rapid, simultaneous changes in catch size, mean trophic level, and FIB values that imply a dramatic increase in the rate of exploitation of Alaskan ecosystems. Some stocks added during this expansion were quickly overfished, notably Pacific ocean perch and some crustacean stocks (Orensanz et al. 1998). However, high industrial rates of exploitation have generally been sustained in recent decades. To that extent, Alaska serves as an example of successful management of industrial fisheries that contrasts with the North Atlantic example. Important research questions center on unforeseen consequences of current management practices, which might eventually result in either reduction in commercial fisheries catches or unacceptable ecological harm from fisheries. Progress in answering those questions in Alaska and other regions may be helped by recognizing that the fishing down the food web paradigm is not a universally applicable model for understanding changes in the composition of commercial fishery catches.

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Impacts of road access on lake trout (*Salvelinus namaycush*) populations: regional scale effects of overexploitation and the introduction of smallmouth bass (*Micropterus dolomieu*)

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Abstract: In lake trout (*Salvelinus namaycush*) lakes of northeastern Ontario, Canada, aerial surveys of fishing activity on individual lakes ($N = 589$) and quantitative gillnet surveys ($N = 65$) were used to assess the effects of road access on angling effort and the presence of introduced smallmouth bass (*Micropterus dolomieu*). Angling effort, particularly during the open-water season, was highest and often exceeded estimated sustainable levels on lakes with good road access. Approximately 25% of the remote lakes also received excessive pressure during the winter season. Angler numerical responses to lake trout abundance were detected in remote lakes, but not in road-accessible lakes. Smallmouth bass were more prevalent in lakes with road access and human settlement (either cottages or lodges), supporting the theory that they were introduced into these lakes. Lake trout populations were depleted throughout much of the study range. Even without road access or smallmouth bass, lake trout abundance was still 47% lower than in unexploited reference lakes. When bass and (or) road access were present, lake trout abundance decreased by 77%. Remote lake trout populations in this area are clearly vulnerable to the negative impacts of improved access, a vector for both overexploitation and species introductions.

Résumé : Des inventaires aériens de l'activité de pêche sur des lacs individus ($N = 589$) et des inventaires quantitatifs au filet maillant ($N = 65$) nous ont servi à évaluer les effets de l'accès routier sur l'effort de pêche sportive et sur la présence d'achigans à petite bouche (*Micropterus dolomieu*) introduits dans des lacs à touladis (*Salvelinus namaycush*) du nord-est de l'Ontario, Canada. L'effort de pêche, particulièrement durant la période d'eau libre, est le plus élevé dans les lacs facilement accessibles par la route et il dépasse souvent le niveau admissible estimé. Environ 25 % des lacs éloignés subissent aussi une pression excessive durant la saison d'hiver. On remarque une relation entre le nombre de pêcheurs et l'abondance des touladis dans les lacs éloignés, mais pas dans les lacs accessibles par la route. Les achigans à petite bouche sont plus présents dans les lacs à accès routier et à présence humaine (chalets ou auberges), ce qui laisse croire qu'ils ont été introduits dans ces lacs. Les populations de touladis sont réduites dans presque toute la région d'étude. Même en l'absence d'accès routier et d'achigans à petite bouche, l'abondance des touladis est tout de même de 47 % inférieure à celle des lacs témoins non exploités. Quand il y un accès routier et (ou) présence d'achigans, l'abondance des touladis est réduite de 77 %. Les populations éloignées de touladis sont visiblement vulnérables aux impacts négatifs de l'amélioration de l'accès routier, un vecteur représentatif à la fois de la surexploitation et de l'introduction d'espèces.

[Traduit par la Rédaction]

Introduction

Many of Canada's recreational fisheries have shown the effects of overexploitation (Post et al. 2002) or the impacts of invasive or introduced species (Vander Zanden et al. 2004*b*). However, the rugged terrain and relatively low human settlement density in remote areas of the Boreal Shield region of Ontario give the impression that such areas would likely have many unexploited fish stocks and unaltered aquatic communities. In fact, little of northern Ontario can still be considered remote. All-terrain vehicles and a network of forestry and other roads now make all but a few protected areas accessible to anglers (fig. 1 in Gunn and Sein 2000). With improved access, widely distributed sportfish populations, such as lake trout (*Salvelinus namaycush*), a species that occurs in less than 1% of the lakes (Martin

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and Olver 1976), now appear to require management planning and action at a broad landscape level rather than at the traditional individual-lake level (Lester et al. 2003).

Several life history characteristics of lake trout, including its late maturity and low fecundity (Martin and Olver 1980), make this large-bodied sportfish highly vulnerable to overexploitation (Post et al. 2002). The high susceptibility of lake trout populations to overharvest has been demonstrated using life history based simulation models (Shuter et al. 1998). Direct observations of lake trout population decline in response to angling pressure have also been reported. Gunn and Sein (2000) estimated that over 70% of a population in one lake was harvested after only a few months in an open-access fishery. However, extrapolating from case histories to regional effects of exploitation is difficult because many factors contribute to an angler's choice of location (Aas et al. 2000; Beard et al. 2003). Moreover, lake trout fisheries are influenced by lake-specific biotic factors that affect angling catch rates, such as the presence or absence of other competitive fish species (Goddard et al. 1987).

In addition to excessive angling exploitation, the adverse impacts of invasive or introduced species are now threatening many indigenous fish populations (Rahel 2002). With respect to lake trout populations of northeastern Ontario, the introduction of centrarchids into inland lakes appears to be a potentially serious problem (Vander Zanden et al. 1999*a*, 1999*b*). For example, the introduction of smallmouth bass (*Micropterus dolomieu*) can significantly alter the abundance and availability of littoral zone prey fish species that are important seasonal forage for lake trout (MacRae and Jackson 2001; Jackson 2002). Although stocking of centrarchids has been conducted by management agencies to create alternate angling opportunities, many introductions are unplanned, occurring either by dispersal through connected waterways (Jackson and Mandrak 2002) or through introductions by anglers or lake residents (Lintermans 2004). Warm-water species such as smallmouth bass are also more likely to be successful in areas at the northern limit of their range because of climate warming (Jackson and Mandrak 2002; Sharma and Jackson 2008).

The objectives of our study were threefold: (*i*) to investigate the factors that influence angling effort for lake trout over a broad landscape scale, particularly in relation to road access, proximity to human settlement, and the abundance of trout in particular lakes; (*ii*) to assess if smallmouth bass had been introduced and how patterns of human usage, such as roads and cottages and lodges, have affected the distribution of smallmouth bass in our study area; and (*iii*) to assess how introduced bass combined with angling effort have affected lake trout abundance.

Materials and methods

Our study area encompassed northeastern Ontario, Canada, where over 900 lake trout lakes exist, representing approximately one-third of the total number of lake trout lakes in the province and approximately 8% of the global resource (Gunn et al. 2004; Selinger et al. 2006). We collected fishery-dependent (angling effort) and fishery-independent (index netting) data and assessed the native range of smallmouth bass in this region to address the objectives of this study.

Aerial surveys of angling effort

Estimates of angling effort were obtained by aerial surveys of 589 lakes (herein referred to as the effort lakes) across northeastern Ontario between 2001 and 2003 (Fig. 1). This cost-effective method compares favourably with traditional on-the-water or access-point creel surveys (Lockwood and Rakoczy 2005) and has been recommended for collecting angling effort data in Ontario (Lester and Dunlop 2004).

Effort surveys were stratified by season (open-water season and winter) and day type (weekday versus weekends and holidays). One midday flight between 1000 and 1400 was conducted each week, alternating between day types. Lakes were chosen based on flight lines that allowed for the maximum number of samples possible. Angling effort (E, h·year^{-1}) was calculated by season (j) for each water body as

$$(1) \qquad E_j = \frac{\mathrm{MAC}_j \cdot T_j \cdot p_j \cdot D_j}{K_{m,j}}$$

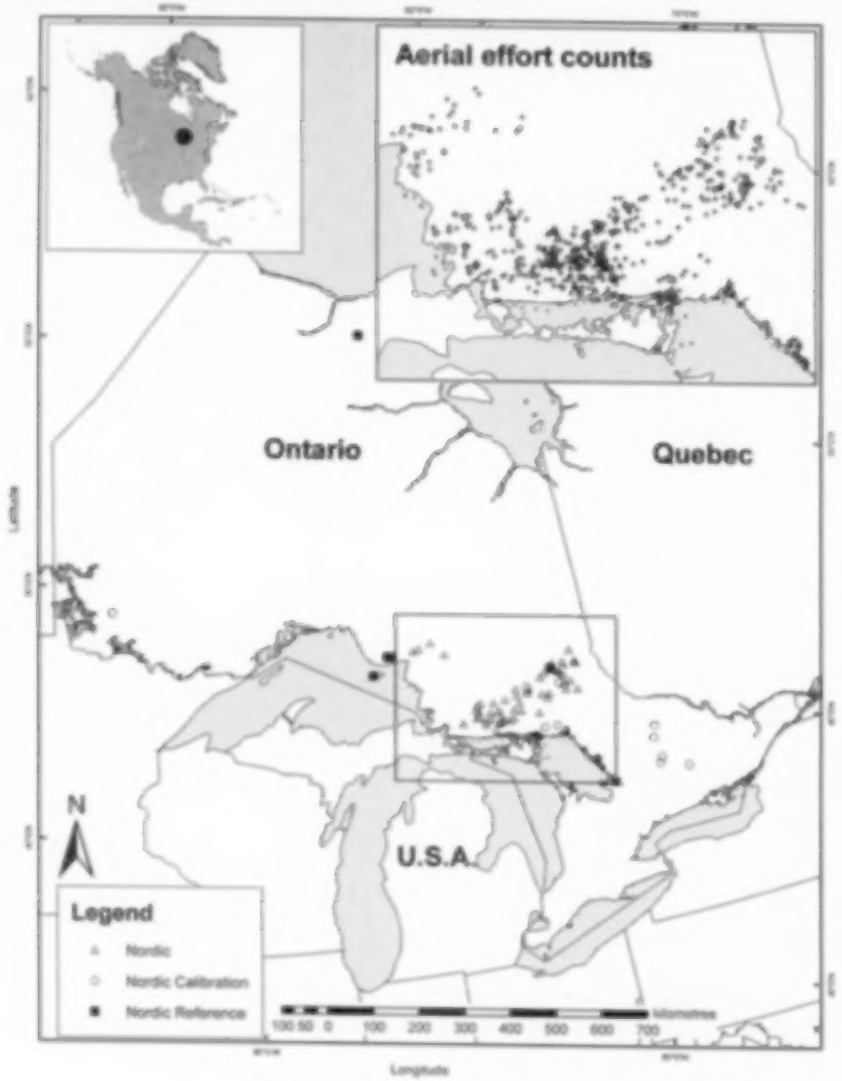
where MAC is mean midday activity count, T is the length of the angling day (assumed to be 14 and 10 h in the open-water season and winter, respectively), p is party size (correcting for instances in which parties were counted rather than individual anglers; occupied ice huts were assumed to have a party size of two), and D is the number of fishing days in the season. Season and day type specific correction factors (K_m) were developed from appropriately stratified roving creel data (Lester and Dunlop 2004; Parker et al. 2006) and applied to correct for changing fishing activity during the course of the day. During the open-water season, K_m values were 1.3 and 1.1 on weekdays and weekends–holidays, respectively. Winter correction factors were 1.5 and 1.2 on weekdays and weekend–holidays, respectively. Greater detail of aerial effort survey methods is provided in Selinger et al. (2006). Effort was then divided by lake surface area to obtain angling intensity (h·ha^{-1}). In addition, estimated angling intensity at maximum sustainable yield (E_{MSY}, h·ha^{-1}) was calculated as per Lester and Dunlop (2004), derived from the model presented in Shuter et al. (1998):

$$(2) \qquad E_{\mathrm{MSY}} = 10^{0.0054 + \frac{1.557}{\mathrm{Area}^{0.116}} - 0.222 \log_{10}\mathrm{TDS} + 0.073 \log_{10}\mathrm{Area} \log_{10}\mathrm{TDS}}$$

where E_{MSY} is related to lake surface area (Area, ha) and total dissolved solids (TDS, mg·L^{-1}). All water quality parameters (including TDS) were measured between 2001 and 2004 by water sampling shortly after ice-out (April).

Each effort lake was classified as to the type of access. Access was defined as highway, primary road, secondary road, tertiary road, trail, remote (greater than 500 m from any type of road or trail access), or restricted (former forestry roads or trails with access blocked or bridges eliminated). The closest population centres of at least 5000 and 50 000 people were also determined for each lake. Using the combination of roads needed to access the lake and assigned travel speeds for each type of road (highway, 100 km·h^{-1}; primary, 80 km·h^{-1}; secondary, 40 km·h^{-1}; tertiary, 20 km·h^{-1}; trail, remote, and restricted, 2 km·h^{-1}), the amount of time needed to access the lake was calculated from each population centre.

Fig. 1. Map of Ontario, Canada, showing location of Nordic reference lakes, study lakes, and calibration lakes (see Appendix A). Enlarged section of northeastern Ontario shows locations of lakes surveyed for angling effort.



Fish community assessment

A subset of 59 of the effort lakes was chosen for fish community analyses (Fig. 1). Lakes were randomly selected from three surface-area categories (50–150 ha, 150–400 ha, 400–20000 ha) in proportion to the number of all known lake trout lakes by these same size categories within the region using the Ontario Ministry of Natural Resources Aquatic Habitat Inventory (AHI) database; see atlas of lakes in northeastern Ontario in Gunn et al. (2004). We avoided lakes that had any special angling regulations in place (base regulation: three fish of any size per day; 1 January to 30 September at the time of data collection) because both fish abundance and anglers' choice of locations to fish can be affected by regulations (Cox et al. 2003).

Between 2000 and 2004, whole-lake fish community assessments were conducted using the Nordic index netting method. The Nordic method is based on a depth-stratified, random-sampling design that takes place during the period of summer thermal stratification (Appleberg 2000; Morgan and Snucins 2005). The sampling effort in each depth stratum (<3 m, 3–5.9 m, 6–11.9 m, 12–19.9 m, 20–34.9 m, 35–49.9 m, and 50–75 m) is proportional to the volume of water in each stratum, thus providing a whole-lake, volume-weighted estimate of entire fish community relative abundance and relative biomass. Benthic gillnets (30 m long × 1.5 m high) with randomly arranged (but identical between nets) seamless panels of geometrically increasing mesh sizes (5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, and 55 mm

(square measure)) were set at random orientations to shore between 1800 and 2000 and lifted between 0600 and 0800 on the following morning. All fish were identified to species and measured for fork length (mm), total length (mm), and round weight (g). We used the Nordic results to determine the presence or absence of smallmouth bass and pelagic prey species (including rainbow smelt (*Osmerus mordax*), lake whitefish (*Coregonus clupeaformis*), and cisco (*Coregonus artedi*)) and to determine lake trout relative abundance (Appendix A). In addition, six reference lakes for which exploitation was considered either nil or minimal were surveyed (Fig. 1). Four of the reference lakes (Mishi, Mishibishu, Katzenbach, and Whitepine) were long-term fish sanctuaries (i.e., no fishing allowed for >10 years), and two lakes (Michi and Hawley) were extremely remote with very restricted access.

Assessment of smallmouth bass introduction

Historical presence or absence of smallmouth bass was determined for the netting assessment lakes that had smallmouth bass present. First, we used the AHI database consisting of lake survey information compiled from standard qualitative assessment methods conducted from the 1960s to the 1980s. These surveys used 120 m gangs of gillnets (38, 51, 64, 76, 89, 102, 114, and 127 mm (stretched measure)) and minnow traps set overnight (Dodge et al. 1985). The AHI surveys were a rapid assessment method usually involving only a single sampling effort per lake (duration 2–5 days) but were shown by Bowlby and Green (1987) to be very effective at detecting the presence of the larger, more common fish species. These authors showed that smallmouth bass were one of the species more easily captured with the AHI gear and reported a 85% effectiveness of detecting smallmouth bass when they are known to be present in a water body. Of the remaining lakes in our survey that had bass during the AHI surveys, lake elevation and broad geographical area were used to assess whether bass populations were native or non-native based on the study of Robbins and MacCrimmon (1974). They suggest that populations along the north shore of Lake Huron, north of Lake Wanapitei (Sudbury), or near Temagami would only be native in lakes below 237, 267, and 300 m above sea level, respectively.

Current information on the presence or absence of cottages or tourist lodges was also determined for these lakes using land-use permit and private land patent data from the AHI database and the Natural Resource Values Information System database, and in some cases, information was updated by field crews during netting assessments.

Statistical analyses

Analyses of variance (ANOVA) were used to test for differences in angling intensity ($h \cdot ha^{-1}$, log-transformed) among access types. Post hoc comparisons were done using Tukey's tests.

We used multiple regression to determine the relative influence of lake surface area (log-transformed), access type, and travel time to each lake (log-transformed) from population centres of 5000 and 50 000 people on angling effort ($h \cdot year^{-1}$). Travel time to each lake was weighted proportional to (i.e., multiplied by) the inverse of the number of residents of the specific population centre under consideration, because we assumed that a large population was likely to exert more pressure than a small population for a given travel time to a lake. Type III sums of squares were used to calculate partial F statistics to assess the significance of each variable above and beyond the other variables entered into the model (Spitvak et al. 2007). On the subset of effort lakes used for population assessments, we used ordinary linear regression to test the angler numerical response (E_p, log-transformed) to our Nordic index of lake trout abundance (catch per unit effort (CPUE, (log-transformed)); Appendix A). For this analysis, we excluded lakes with no effort because we were interested in lake trout abundances that actually attracted anglers. We assessed the power of nonsignificant statistical tests using the methods outlined in Zar (1999) and homogeneity of variances using Levene's test.

Analyses of contingency tables were done using chi-square statistics (Zar 1999). Specifically, we tested whether the proportion of lakes fished above or below E_{MSY} were more frequent in any given access type.

We also tested the hypothesis that the presence of smallmouth bass was affected by road access and the presence of cottages or lodges using log-linear methods (Zar 1999). Here, lakes with highway, primary, secondary, and tertiary road access were grouped as road-accessible lakes, whereas lakes with trail, remote, or restricted access were grouped as remote lakes.

Finally, we tested for differences in chemical, fish community, or habitat-related variables that may explain the presence of smallmouth bass or roads using ANOVA. We also tested how bass presence or absence and road access vs. remote access interacted to affect lake trout abundance using a factorial ANOVA. Again, access types were grouped into the more broad categories of road access and remote. Post hoc analysis was done with a Tukey's test. Quantification of the statistical power of additive effects of road access and bass was performed using analytical procedures outlined in Gerow (2007). All other statistical tests were performed using Statistica (version 6; StatSoft, Inc. 2001) and considered significant at $P < 0.05$.

Results

Factors affecting angling intensity and effort

Total angling intensity estimated from the aerial surveys ranged from 0 to 92 $h \cdot ha^{-1}$; intensities ranged from 0 to 36 $h \cdot ha^{-1}$ during the winter and from 0 to 68 $h \cdot ha^{-1}$ during the open-water season (Table 1). Sample sizes of midday activity counts (i.e., the number of flights) for individual lakes ranged from 10 to 64.

There were significant differences in angling intensity among access types ($F_{[0.579]} = 5.27$, $P < 0.001$; Fig. 2) during the open-water season. Remote lakes received less pressure than primary and secondary road accessible lakes. During the winter, there was no difference in angling intensity among access types ($F_{[0.575]} = 1.17$, $P = 0.32$; Fig. 2). The proportion of lakes angled beyond the estimated sustainable levels (E_{MYS}) was higher for lakes with road access than without road access ($\chi^2_6 = 37.42$, $P < 0.001$). For example, 63% of highway-accessed lakes were angled at inten-

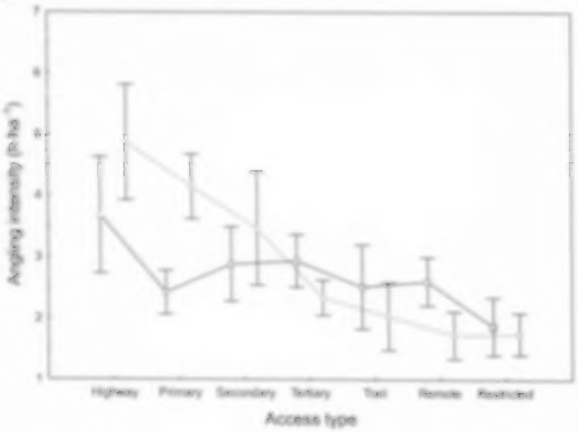
Table 1. Sample sizes (N), range in number of midday activity counts (MAC) from individual water bodies, and mean (range in parentheses) effort intensities ($h \cdot ha^{-1}$) by surface area category from 589 lakes surveyed by aerial methods.

Surface area category	N	MAC range	Open-water season effort intensity ($h \cdot ha^{-1}$)	Winter effort intensity ($h \cdot ha^{-1}$)
<150	377	10–64	2.4 (0–68.2)	3.0 (0–36.3)
150–800	129	17–60	2.6 (0–18.5)	2.4 (0–17.0)
>800	83	17–40	3.8 (0–32.0)	1.9 (0–19.6)

Table 2. Multiple regression models predicting open-water season and winter angling effort ($h \cdot year^{-1}$) from lake surface area, access type, and time to lake (TTL) from the closest population centres of 5000 (TTL 5000) and 50 000 (TTL 50 000) people.

Model	Variable	Partial F	P	Partial r^2
Open-water season	Surface area (ha)	303.04	<0.001	0.44
	Access type	14.71	0.001	0.02
	TTL 5000	12.57	<0.001	0.01
	TTL 50 000	4.69	0.03	<0.01
Winter	Surface area (ha)	92.27	<0.001	0.18
	TTL 50 000	15.27	0.001	0.05
	TTL 5000	5.38	0.02	0.01

Fig. 2. Open-water season (○, dotted line) and winter (□, solid line) angling effort intensity ($h \cdot ha^{-1}$) by access type. Error bars represent ± 1 standard error.



sities beyond E_{MSY}, whereas only 26% of remote lakes were angled beyond the estimated sustainable level.

Multiple regression revealed distinct seasonal patterns in angling effort ($h \cdot year^{-1}$) related to road accessibility and proximity to population centres (Table 2). During the open-water season, surface area accounted for the majority of variation in angling effort (partial $F_{[1,452]} = 303.04$, $P < 0.001$, partial $r^2 = 0.44$). The type of access was a significant term in the regression model, although it accounted for little additional variation (partial $F_{[1,452]} = 14.71$, $P = 0.001$, partial $r^2 = 0.02$). Similarly, travel times to a lake from population centres of both 5000 and 50 000 people were significant in the model; however, they explained little further variation (5000, partial $F_{[1,452]} = 12.57$, $P < 0.001$, partial $r^2 = 0.01$; 50 000, partial $F_{[1,452]} = 4.69$, $P = 0.03$, partial $r^2 < 0.01$). Patterns differed slightly during the winter; surface area still accounted for the majority of explained variation in angling effort (partial $F_{[1,447]} = 92.27$, $P < 0.001$, partial $r^2 = 0.18$). Time to a lake from the closest population of at least 50 000 explained a further 5% of the variation (partial $F_{[1,447]} = 15.27$, $P = 0.001$, partial $r^2 = 0.05$), and an additional 1% was explained by the time to a lake from the closest population centre of 5000 people (partial $F_{[1,447]} = 5.38$, $P = 0.02$, partial $r^2 = 0.01$).

Angler numerical responses to lake trout abundance only occurred in remote lakes (Figs. 3*a*, 3*b*). During the open-water season, angling intensity ($h \cdot ha^{-1}$) was significantly related to lake trout abundance ($r^2 = 0.30$, $P = 0.014$) in remote lakes, but intensity and abundance were not significantly related in road-accessible lakes ($r^2 = <0.01$, $P = 0.96$; Fig. 3*a*). Similar results were observed during the winter, where angling intensity increased with lake trout abundance on remote lakes only (remote, $r^2 = 0.31$, $P = 0.003$, road-accessible, $r^2 = 0.09$, $P = 0.28$; Fig. 3*b*). Our statistical power to detect a significant angler numerical response in the open-water season and winter was 5% and 19%, respectively. Variances were homogenous among the models ($P > 0.05$).

Assessment of smallmouth bass introduction

In the subset of lakes where bass were present in the Nordic assessment ($N = 16$), historical survey records from the AHI program suggest that they had not been present in 50% (8) of these lakes during past decades. Of the remaining eight lakes, bass populations were found in lakes at elevations that were too high to be accounted for by natural post-glacial colonization. In addition, there were no consistent confounding physical, chemical, or biotic factors that would explain bass presence in the study lakes. Lake trout lakes

Fig. 3. Angling intensity (h·ha^{-1}) versus lake trout (*Salvelinus namaycush*) catch per unit effort (CPUE, number of fish·net^{-1}) during (*a*) winter and (*b*) the open-water season. Fitted curves represent significant log–log relationships for remote lakes (○) only. Relationships for road-accessible lakes (■) were not significant.

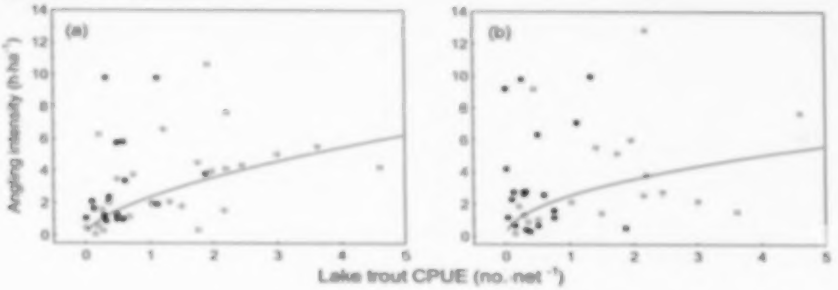


Table 3. Means (±95% confidence interval) of physical, productivity, fish community, and thermal variables from reference lakes and lakes without and with smallmouth bass (*Micropterus dolomieu*).

	Lakes				
Variables	Reference	Without bass	With bass	*F*	*P*
Physical variables					
Surface area (ha)	455 (45, 865) a (n = 6)	174 (19, 329) a (n = 42)	446 (216, 676) a (n = 16)	2.33	0.105
Maximum depth (m)	49.3 (37.1, 61.5) b (n = 6)	31.9 (27, 36.8) a (n = 38)	28.2 (21.3, 35.1) a (n = 16)	4.53	0.015
Elevation (m)	329 (273, 385) ab (n = 6)	375 (352, 398) b (n = 38)	324 (292, 356) a (n = 16)	3.79	0.028
Productivity variables					
Total dissolved solids (μg·L^{-1})	47.0 (–2.3, 96.3) a (n = 6)	36.8 (17.5, 56.1) a (n = 40)	21.4 (15.2, 27.6) a (n = 14)	0.52	0.599
Phosphorous (μg·L^{-1})	n/a	6.3 (5.3, 7.3) a (n = 39)	6.2 (4.7, 7.7) a (n = 14)	0.02	0.895
Secchi depth (m)	5.8 (1.2, 10.4) a (n = 6)	6.7 (5.6, 7.8) a (n = 29)	5.8 (4.3, 7.3) a (n = 14)	0.61	0.547
Fish community variables					
Species richness	9 (5, 13) ab (n = 6)	9 (8, 10) a (n = 42)	11 (9, 13) b (n = 16)	3.15	0.050
Relative fish community biomass (g·net^{-1})	2966 (2204, 3728) b (n = 6)	2167 (1738, 2596) ab (n = 42)	1915 (1627, 2203) a (n = 16)	3.44	0.038
Pelagic prey presence (%)	83 (n = 6)	33 (n = 42)	74 (n = 16)	—	—
Thermal variables					
Growing degree days	1408 (1307, 1509) b (n = 6)	1701 (1663, 1739) a (n = 42)	1696 (1640, 1752) a (n = 16)	15.27	<0.001
Thermocline depth (m)	4.3 (2.7, 5.9) a (n = 6)	4.3 (3.6, 5.0) a (n = 29)	4.9 (3.9, 5.9) a (n = 13)	0.47	0.629

Note: Species richness (defined as the number of species present) and relative fish community biomass were determined from Nordic surveys. Growing degree days were calculated from the year in which the Nordic survey was conducted (Terry Marshall, Northwest Science and Technology, Ontario Ministry of Natural Resources, Thunder Bay, Ontario, Canada, personal communication). Thermocline depth was the depth at the beginning of the thermocline measured during the Nordic survey. *F* statistics and *P* values are from analyses of variance comparing the groups. Statistically similar values are denoted by the same lowercase letter. n/a, not available.

with bass had similar surface areas, TDS, total P, Secchi depth, growing degree days, and thermocline depth as lakes without bass (Table 3). However, lakes with bass were at lower elevations (although still above the elevation restrictions to natural bass postglacial dispersal) and had, on average, two more species (one of which can be attributed to bass). In contrast, the presence of smallmouth bass was related to the presence of cottages and (or) lodges and road

Table 4. Number of lakes sampled with (present) and without (absent) smallmouth bass (*Micropterus dolomieu*) by road accessibility and presence or absence of cottages or lodges.

	Road accessible		Remote	
Smallmouth bass	Cottage or lodge present	Cottage or lodge absent	Cottage or lodge present	Cottage or lodge absent
Present	3 (0.63)	7 (–1.06)	3 (–0.25)	3 (–2.72)
Absent	1 (–0.63)	14 (1.06)	4 (0.25)	23 (2.72)

Note: Values in parentheses are standard residuals from log-linear analysis.

Table 5. Means (95% confidence interval) of physical, productivity, fish community, and thermal variables from reference, remote, and road-accessible lakes.

	Lakes				
Variables	Reference	Remote	Road-accessible	*F*	*P*
Physical variables					
Surface area (ha)	455 (45, 865) a (n = 6)	174 (105, 243) a (n = 33)	340 (26, 654) a (n = 25)	1.79	0.175
Maximum depth (m)	49.3 (37.1, 61.5) b (n = 6)	32.3 (25.6, 39.0) a (n = 29)	28.2 (24.3, 32.1) a (n = 25)	6.80	0.002
Elevation (m)	329 (273, 385) b (n = 6)	375 (356, 394) a (n = 29)	371 (348, 394) a (n = 25)	18.95	<0.001
Productivity variables					
Total dissolved solids ($\mu g \cdot L^{-1}$)	47.0 (–2.3, 96.3) a (n = 6)	19.2 (15.9, 22.5) a (n = 31)	51.7 (10.6, 92.8) a (n = 23)	3.16	0.050
Phosphorous ($\mu g \cdot L^{-1}$)	n/a	6.3 (5.3, 7.3) a (n = 31)	6.2 (4.7, 7.7) a (n = 22)	0.02	0.895
Secchi depth (m)	5.8 (1.2, 10.4) a (n = 6)	6.5 (4.9, 8.1) b (n = 22)	6.0 (5.1, 6.9) a (n = 21)	8.59	<0.001
Fish community variables					
Species richness	9 (5, 13) a (n = 6)	8 (7, 9) a (n = 33)	10 (8, 12) a (n = 25)	0.51	0.605
Relative fish community biomass ($g \cdot net^{-1}$)	2966 (2204, 3728) b (n = 6)	1946 (1674, 2218) a (n = 33)	2058 (1692, 2424) a (n = 25)	9.57	<0.001
Pelagic prey presence (% of lakes)	83 (n = 6)	42 (n = 33)	44 (n = 25)	—	—
Thermal variables					
Growing degree days	1408 (1307, 1509) b (n = 6)	1695 (1648, 1742) a (n = 33)	1696 (1658, 1734) a (n = 25)	14.35	<0.001
Thermocline depth (m)	4.3 (2.7, 5.9) a (n = 6)	4.5 (3.6, 5.4) a (n = 21)	4.5 (3.6, 5.4) a (n = 21)	0.02	0.979

Note: Species richness (defined as the number of species present) and relative fish community biomass were determined from Nordic surveys. Growing degree days were calculated from the year in which the Nordic survey was conducted (Terry Marshall, Northwest Science and Technology, Ontario Ministry of Natural Resources, Thunder Bay, Ontario, Canada, personal communication). Thermocline depth was the depth at the beginning of the thermocline measured during the Nordic survey. *F* statistics and *P* values are from analyses of variance comparing the groups. Statistically similar values are denoted by the same lowercase letter. n/a, not available.

access (χ^2_1 = 17.97, P = 0.001). Disproportionately more lakes that had both road access and cottages or lodges had smallmouth bass present. Fewer remote lakes that lacked cottages or lodges had bass (Table 4).

Effects of roads and smallmouth bass on lake trout

There were no obvious differences in lake characteristics among reference, remote, or road-accessible lakes. Reference, remote, and road-accessible lakes were similar in lake size, productivity (total P, TDS), thermocline depth, and fish species richness (Table 5). Even though reference lakes were deeper, at lower elevations, had cooler climate conditions (growing degree days), and had higher total fish biomass than remote and road-accessible lakes, the latter two lake types were still similar to each other in these characteristics.

Lake trout relative abundance differed significantly in relation to road access and smallmouth bass presence. In the six reference lakes (no road access, no bass, and no angling), the mean CPUE was 2.6 fish·net^{-1}. There was a significant interaction between the presence of smallmouth bass and road access on lake trout CPUE (ANOVA, $F_{[1,55]}$ = 6.68, P = 0.012; Fig. 4; Table 6). In remote lakes without

Fig. 4. Lake trout (*Salvelinus namaycush*) catch per unit effort (CPUE, number of fish·net^{-1}) by access type in lakes with (hatched bars) and without (solid bars) smallmouth bass (*Micropterus dolomieu*). Reference lakes had no road access or smallmouth bass and minimal or no angling. Error bars represent ± 1 standard error.

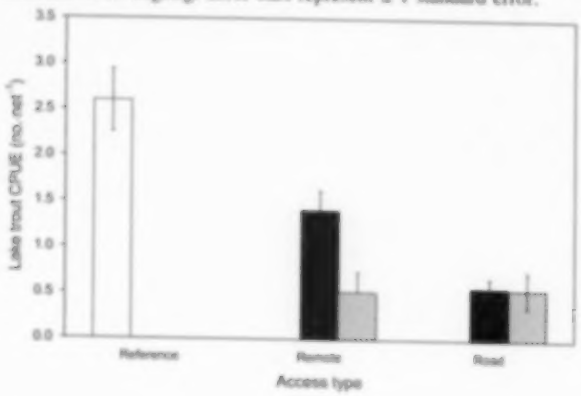


Table 6. Two-way analysis of variance (ANOVA) results of the effect of smallmouth bass presence and road access on lake trout abundance in 59 lakes in northeastern Ontario, Canada.

Effect	SS	df	MS	*F*	*P*
Smallmouth bass	16.76	1	16.76	14.02	<0.001
Access	0.69	1	0.69	0.58	0.449
Smallmouth bass × access	7.99	1	7.99	6.68	0.012
Error	65.75	55	1.20		

Note: SS, sum of squares; df, degrees of freedom; MS, mean squares; *F*, *F* statistic; *P*, probability.

smallmouth bass, lake trout CPUE was 47% (1.4 fish·net^{-1}) lower than in reference lakes, suggesting that this was the effect of general or background levels of exploitation in the region. In the presence of smallmouth bass, there was a significant further reduction to 77% fewer fish per net (0.6 fish·net^{-1}). Observed lake trout CPUE was similar in road-accessible lakes with (0.5 fish·net^{-1}) and without (0.6 fish·net^{-1}) smallmouth bass and statistically similar to remote lakes with bass. The power to detect the additive detrimental effect of road access and bass (i.e., the observed 17% reduction) in lake trout abundance was 3%.

Discussion

Factors affecting angling effort

Although case studies of specific lakes have shown that improved access drastically increases angling effort (Gunn and Sein 2000), our survey study demonstrates how extensive this effect is over a very broad study area, an area that includes >50% of the known lake trout lakes in northeastern Ontario. We found that fishing intensity increased with the quality or ease of the access (from paved highway to rough trails or no direct access), but this effect was only significant in the open-water season. During the winter angling season, there were no significant differences among access categories, showing that snowmobiles and all terrain vehicles have now made the entire region a readily accessible resource.

More than half of the easily accessed (e.g., highway) lakes were angled beyond estimated sustainable levels, but remote lakes were also heavily used, with more than 25% of them receiving angling effort above the estimated maximum sustainable level. Management strategies designed to limit access or maintain "remoteness" of these Boreal Shield ecosystems will therefore have only limited success in preventing overexploitation. Maintaining sustainability in other easily accessed salmonid fisheries has proved difficult despite restrictive harvest regulations (Parker et al. 2007). Limited-access fisheries (i.e., reducing total harvest) have been suggested as one of the only truly effective management solutions to limit overexploitation in such areas (e.g., Lester et al. 2003).

The quality of the fishery, in this case measured as the abundance of lake trout in the lake, did affect fishing effort expended by anglers, but angling effort tracked CPUE abundance only in remote areas. This finding suggests that improved access leads to a shift in the "predator–prey" response of anglers to fish abundance (Cox et al. 2003; Post et al. 2008). The increased ease of access (e.g., decreased time spent foraging) appeared to compensate for decreased fish abundance (e.g., lower quality food patch) in the readily accessible lakes. In contrast, when anglers must expend more energy to reach remote lakes, they deliberately balance this deficit by searching for the highest quality fisheries. Post et al. (2008) reported a similar finding from rainbow trout (*Oncorhynchus mykiss*) fisheries in the interior of British Columbia. An alternate explanation for our observations is that anglers in remote areas display self-regulation and simply move on to higher quality lakes once fish abundance declines by some detectible level in the fishery (Hansen et al. 2000). This situation would help in maintaining lake trout stocks in remote lakes by allowing time to recover before intensive fishing occurs again. In contrast, in the easily accessible lakes with high fishing pressure, self-regulation of the fishery is far less effective. Catch rates are often independent of the initial decline in lake trout populations (Shuter et al. 1998), allowing road-accessible lakes to rapidly approach and perhaps stay in a collapsed state (Gunn and Sein 2000).

Our results suggest that angling effort is strongly related to the type of access available, but only weakly related to the proximity of population centres. Other studies have suggested strong relationships between effort and distance to population centres (Post et al. 2002, 2008). In our region, linear distances are likely an inappropriate measure because forestry roads can be extremely convoluted and of varying quality along their lengths. We therefore chose to represent our measure of accessibility by the time spent traveling to a given lake. We also considered the influence of up to two different population centres on the effort applied to each lake, rather than the influence of one comparatively large population centre on each lake as in Post et al. (2008). Another confounding factor that we could not account for was influence of angler participation rates in cities or towns of differing population size. Based on the resource-based nature of the community types in northeastern Ontario, we would expect that the declining relationship in participation

rates with population size derived in Post et al. (2008) would be less pronounced in our study. We attempted to account for this by weighting travel times in favour of large communities.

Assessment of smallmouth bass introduction

Although smallmouth bass are native to portions of the Shield area of Ontario (Hubbs and Lagler 2004), they have also been introduced widely throughout Ontario. Of the estimated 2421 smallmouth bass populations in Ontario, more than 800 were established through introductions, and bass now occupy lakes and rivers at least as far north as Timmins (Kerr and Grant 2000). Several recent studies show that bass introductions into new waters are still occurring (Snucins and Gunn 2003; Lippert et al. 2007). All of the lakes with bass in our study were found either where they were absent during the AHI surveys or in lakes at elevations that were above the levels that would have allowed natural postglacial colonization (Robbins and MacCrimmon 1974). Mean elevation of our lakes with bass was 300 m, whereas the highest elevation from Robbins and MacCrimmon (1974) where bass would occur naturally was 300 m. In addition, we have shown a strong association of the presence of bass with road accessibility and the presence of cottages and (or) lodges. Roads have been identified as major vectors for the inland spread of several exotic species (Bossenbroek et al. 2001; MacIsaac et al. 2004). More specifically, studies of factors affecting smallmouth bass introductions into other lake trout lakes in Ontario have identified road accessibility as a likely factor in explaining their current distribution (Vander Zanden et al. 2004*a*, 2004*b*). Other factors in the Vander Zanden et al. (2004*a*) model of bass distribution, such as lake surface area, were similar among our study lakes with and without bass.

Effect of angling effort and introduced smallmouth bass on lake trout abundance

In our study, road access was clearly associated with two stressors that impact lake trout populations: high angling effort and the presence of smallmouth bass. However, even in remote lakes without bass, lake trout abundance was still only half that of unfished reference lakes. Our aerial surveys also found that fishing effort exceeded sustainable levels in many of the remote lakes. In addition, no physical or chemical characteristics that may affect lake trout abundance (Trippel and Beamish 1993) could account for observed differences in CPUE among reference, road-accessible, or remote lakes. These findings therefore add to a growing body of evidence (Post et al. 2002; Lester et al. 2003) indicating that natural lake trout populations are depleted across much of the Boreal Shield of Ontario and that overexploitation is likely the main cause. Recent experimental studies have reduced concerns about habitat alterations (*e.g.*, sedimentation) as a serious impact on small Shield lakes (Gunn and Sein 2000; Steedman and France 2000; Steedman and Kushneriuk 2000), and there is encouraging evidence that regional acidification is also declining (Gunn and Keller 1990). Earlier studies have also concluded that Ontario lake trout populations are also particularly sensitive to exploitation (Payne et al. 1990; Shuter et al. 1998). The Shuter et al. (1998) simulation model indicated that if a population is exploited beyond a "safe" level of effort, it could sustain itself at a lower equilibrium abundance.

Our results suggest that many of the road-accessible populations may be in a very depleted state, with heavily angled lakes having approximately one-fifth of the lake trout abundance found in reference lakes. The presence of smallmouth bass therefore appears to have an equivalent effect on lake trout as high rates of exploitation. Introduced bass are known to decimate littoral fish communities such as yellow perch (*Perca flavescens*) (Lippert et al. 2007) and cyprinids (Jackson 2002) that provide important seasonal forage for lake trout (Vander Zanden et al. 1999*a*). This effect is often exacerbated by nearshore habitat alterations brought about by human development (Jackson 2002). In these instances, lake trout are forced to consume energetically less profitable food such as zooplankton (Vander Zanden et al. 1999*b*). Vander Zanden et al. (2004*a*) suggest that pelagic forage species should buffer the effects of bass introductions on the trophic status of lake trout; however, our results show that lake trout abundance was still negatively affected even when pelagic prey (cisco, whitefish, or rainbow smelt) were present in the majority (73%) of lakes with bass. Other physical and chemical factors could not explain the differences among lakes with and without bass. The low abundance of lake trout in the presence of smallmouth bass was also not likely attributable to higher angler harvest, because observed angling effort in remote lakes with smallmouth bass was significantly lower than in remote lakes without smallmouth bass (mean without smallmouth bass = 5.6 h·ha^{-1}, mean with smallmouth bass = 1.5 h·ha^{-1}, $t_{33} = 3.23$, $P = 0.003$). We acknowledge that our single point in time sampling does not capture the effects of possible past exploitation and that the lower lake trout CPUE in the remote lakes with bass may be a function of this history. However, the food web alterations that accompany bass introductions could impede recovery if these were once heavily exploited trout populations.

The combined effects of these stressors (i.e., road-accessible lakes with bass) did not appear to result in a further decrease in lake trout abundance. However, we lacked the statistical power in our broad-scale survey approach to adequately address this question. At the observed level of among-lake variation, a sample size of lakes larger than the number of known lake trout lakes in the province would be needed to accurately detect an additive effect.

Our study indicates that lake trout fisheries over a large region of northeastern Ontario are depleted and that roads are an important vector for increased exploitation and the introduction of smallmouth bass, a species that adversely affects lake trout. Our findings concur with similar results or concerns expressed by other authors (Post et al. 2002; Lester et al. 2003; Browne 2007), but in this broad-scale survey, we have added considerable quantitative data to support our interpretation of these changes and trends. The expected expansion of the range of smallmouth bass under climate change and continued extension of road networks into wilderness areas demands that strong measures be taken to protect remaining lake trout populations.

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Appendix A. Nordic index netting calibration

Calibration of the Nordic method to lake trout density was performed between 1999 and 2002 on 10 lakes (see Fig. 1 in main text) where detailed population estimates were available, either by mark–recapture studies ($N = 5$) or by plantings of known numbers of lake trout in former trout lakes where native populations had been completely extirpated ($N = 5$) (Table A1). Hatchery-reared lake trout (both adult brood stock and 1- and 2-year-old juveniles) were released in the lakes 1–2 months before the netting was conducted. One lake (Broker) was surveyed in 2001 and 2002; known numbers of trout were planted each year but identified by unique fin clips. For each calibration lake, the CPUE was calculated only for the lake trout within the size range of fish used in the corresponding population estimate.

Calibration of the Nordic gear to lake trout density tested two models relating catch per unit effort (CPUE) to fish density. Generally, CPUE is related to density (N) by the equation

$$\text{(A1)} \qquad \text{CPUE} = q \cdot N$$

where q is catchability (Ricker 1975). This assumes that catchability is density-independent; therefore, we also tested the model for density-dependent catchability:

$$\text{(A2)} \qquad \text{CPUE} = q \cdot N^b$$

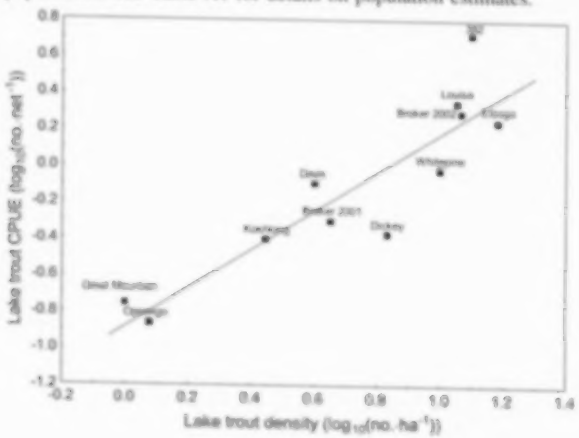
where b is the allometric slope of relationship between CPUE and density.

Table A1. Surface area (ha), lake trout (*Salvelinus namaycush*) size used in population estimate (mm), density (number·ha^{-1}), and source of population estimates for 11 lakes in Ontario, Canada, used in calibration of the Nordic method.

Lake	Surface area (ha)	Size (mm)	Lake trout density (no.·ha^{-1})	Source
Lake 382	37	>127	12.6	Mills et al. 2002
Louisa	567	>300	11.3	B. Munroe, Algonquin Fisheries Assessment Unit, Ontario Ministry of Natural Resources, Whitney, Ont., personal communication
Whitepine	67	>350	10	J. Gunn, Cooperative Freshwater Ecology Unit, Laurentian University, Sudbury, Ont., unpublished data
Davis	34	>370	4	Experimental stocking, E. Snucins and W. Selinger
Great Mountain	198	>560	1	Experimental stocking, E. Snucins and W. Selinger
Dickey	209	>275	6.8	D. Hughes, Haliburton–Hastings Fisheries Assessment Unit, Ontario Ministry of Natural Resources, Bancroft, Ont., personal communication
Koshlong	409	>200	2.8	D. Hughes, Haliburton–Hastings Fisheries Assessment Unit, Ontario Ministry of Natural Resources, Bancroft, Ont., personal communication
Opeongo[a]	1799	>450	1.2	T. Middel, Harkness Fisheries Laboratory, Ontario Ministry of Natural Resources, Algonquin Provincial Park, Ont.
Broker 2001	108	>174	4.5	Experimental stocking, E. Snucins and W. Selinger
Broker 2002	108	>140	11.7	Experimental stocking, E. Snucins and W. Selinger
Elboga	28	>470	15.2	Experimental stocking, E. Snucins and W. Selinger

[a]Only one arm of this lake was surveyed (total lake surface area = 5863 ha); netting results were assumed to be representative of the entire lake.

Fig. A1. Catch per unit effort (CPUE; no.·net^{-1}, log-transformed) from Nordic surveys versus known densities (no.· ha^{-1}, log-transformed) from 10 Ontario lake trout (*Salvelinus namaycush*) populations. See Table A1 for details on population estimates.



Calibration experiments showed a strong positive linear correlation between the log-transformed netting CPUE and known densities of lake trout (also log-transformed) in the test lakes. CPUE explained 81% of the variation in density ($P < 0.001$; Fig. A1). Furthermore, the slope of the allometric equation (1.06 ± 0.17 (standard error of the estimate)) was not significantly different from 1 (*t* test, $t_9 = 0.35$, $P > 0.50$). The final model was

$$\text{CPUE} = 0.13 \cdot N \quad \text{(A3)}$$

where CPUE is the arithmetic mean CPUE (number per net) and N is the population density (number per hectare).

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Performance of artificial neural networks and discriminant analysis in predicting fishing tactics from multispecific fisheries

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Abstract: In the Mediterranean, bottom trawlers are multispecific and frequently apply different fishing tactics (FTs) even during the same fishing trip. Up to four individual FTs were distinguished in the study area where fishermen usually use mixtures of different FTs in daily fishing trips. Identifying the FTs actually performed is a key issue in traditional stock assessment methods. In this paper, we compare the performance of discriminant analysis and artificial neural networks for predicting FTs from the species composition of daily sale bills. We used data on the landings of each vessel from daily sale bills along with information on the FT actually performed, which was obtained by onboard observers who interviewed skippers about the FTs that they planned to employ. Discriminant analysis and artificial neural networks achieved comparable overall results and the success of predictions depended on both the sample size of the different data subsets (balancing) and the similarity between the species composition of different FTs (overlapping). Although the percentage of correct predictions was high for FTs with more than 25 cases, success decreased when the sample sizes were small. In addition, success in predicting mixtures of two different FTs increased with increasing dissimilarity between their corresponding species compositions.

Résumé : Dans la Méditerranée, les chalutiers de fond sont multispécifiques et ils utilisent fréquemment différentes tactiques de pêche (FTs) même durant une seule sortie en mer. Nous avons identifié jusqu'à quatre FTs différentes dans la zone d'étude où les pêcheurs utilisent une combinaison de FTs différentes dans leurs sorties journalières de pêche. L'identification des FTs effectivement utilisées est une donnée essentielle pour les méthodes traditionnelles d'évaluation des stocks. Dans notre étude, nous comparons la performance de l'analyse discriminante et des réseaux de neurones artificiels pour prédire les FTs à partir des compositions d'espèces des factures quotidiennes de vente. Nous utilisons des données sur les débarquements de chaque navire tirées des factures de vente, ainsi que des informations sur les FTs effectivement utilisées obtenues par des observateurs à bord qui ont interrogé les capitaines sur les FTs qu'ils comptaient utiliser. L'analyse discriminante et les réseaux de neurones artificiels fournissent globalement des résultats comparables et le succès des prédictions dépend à la fois de la taille de l'échantillon des différents sous-ensembles de données (équilibrage) et de la similarité de la composition spécifique des différentes FTs (chevauchement). Bien que le pourcentage de prédictions justes soit élevé pour les FTs représentées par plus de 25 cas, le succès décroît lorsque la taille des échantillons est petite. De plus, le succès de la prédiction pour des mélanges de deux FTs différentes augmente en fonction directe de la dissemblance entre leurs compositions spécifiques respectives.

[Traduit par la Rédaction]

Introduction

The Mediterranean demersal fisheries are both multifleet and multispecific, with more than 100 species in their landings (Moranta et al. 2008). In addition, both small-scale and bottom-trawl fisheries are characterized by spatial and temporal variability of their fishing strategies that mainly depend on the bathymetric range and determine both the target species and the demersal communities exploited (Biagi et al. 2002; Colloca et al. 2003; Massutí and Reñones 2005). Identifying fishing tactics (FTs), which are defined as a combination of target species, gear, and fishing location at a given time of the year (Pelletier and Ferraris 2000), is a key point in fisheries showing such heterogeneity of fishing practices. While assessing the relationship between catch and effort is straightforward in monospecific oceanic fisheries directed exclusively at a single target species, for fisheries that use different FTs, a preliminary analysis is necessary to determine the effort exerted directly on specific species. If this first step of identifying the FTs actually per-

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formed is overlooked, then the fishing mortality effectively exerted on specific stocks will not be properly assessed, which may give rise to incorrect management advice.

In the western Mediterranean, bottom trawlers operate along a wide bathymetric range, from the shallow shelf (deeper than 50 m depth) to the middle slope (down to 800–1000 m). Fishing effort is mainly managed by, among other technical measures, controlling fishing time (e.g., maximum of 12 h per day for 5 days a week). This implies daily fishing trips after which the fleet returns to their home port to land their catches. Although this procedure allows fishing effort (catch per day) to be measured in detail, it becomes more complicated to do so when commercial vessels employ different FTs even during the same fishing day, working at distinct depth strata depending on the season, weather conditions, and economic factors (e.g., landing price). Daily sale bills, which contain the catches landed daily by a vessel along with their corresponding sale prices, are then constituted by a highly diverse mixture of species taken at different fishing grounds and consequently reflecting the use of different FTs. However, these catches taken on such different fishing grounds can be identified from daily sale bills because these fishing grounds have distinctive bottoms that are characterized by different assemblages of demersal species (Massutí and Reñones 2005). In the Balearic Islands (western Mediterranean), commercial trawlers employ up to four different FTs, which are associated with the shallow and deep continental shelf and the upper and middle continental slope (Guijarro and Massutí 2006; Ordines et al. 2006). Vessels mainly target striped red mullet (*Mullus surmuletus*) and European hake (*Merluccius merluccius*) on the shallow and deep shelf, respectively. However, these two target species are caught along with a large variety of fish and cephalopod species. The Norway lobster (*Nephrops norvegicus*) and the red shrimp (*Aristeus antennatus*) are the main target species on the upper and middle slope, respectively. The Norway lobster is caught at the same time as a large number of other fish and crustacean species, but the red shrimp fishery is the only Mediterranean fishery that could be considered monospecific. The different FTs used are not considered for managing the trawl fishery, which therefore reduces the efficiency of management measures to regulate the effective fishing mortality exerted on specific stocks. To determine this effective fishing effort properly, analyses of catch per unit effort (CPUE) data from daily sale bills require the FTs actually performed to be identified, and if more than one FT has been carried out, a classification method is needed to identify them from the mixture of species present in the daily sale notes.

Until now, the most common approach for inferring FTs from sale bills has been to cluster them according to the similarity of their species composition; it is assumed that the clusters obtained include the fishing trips in which the same FT was performed (Alemany and Alvarez 2003; García-Rodríguez 2003; Tzanatos et al. 2006). This approach has two important drawbacks: (*i*) there is neither theoretical nor data-driven support to determine the cutoff values of dissimilarity needed to identify the different groups obtained, and therefore, the number of clusters is subjective; and (*ii*) the functional interpretation of the resulting clusters is carried out subsequently, which implies that, in practice, the most common FT in a group is assumed to be the only one performed for all of the samples in that group. In some cases, as a preliminary step, the sale bills corresponding to a predefined period (usually a month) and vessel are pooled together (Poulard and Léauté 2002; Alemany and Álvarez 2003; García-Rodríguez 2003), which implies assuming negligible within-month variability in the FTs of a vessel. However, as previously mentioned, both the target species and the communities exploited may change over time scales that are much shorter than the pooled time period. Even if this preliminary pooling step is not carried out and the daily sale bills are analyzed individually, there is still uncertainty because a single bill actually reflects the results of applying more than one tactic in a single fishing trip. In most cases, raw data are usually submitted to some filtering to reduce noise, such as principal components analysis or other techniques that reduce dimensionality, assuming that the between-bill similarity is captured well within a new space formed by only the first few principal components analysis axes.

A first alternative to these previous approaches is discriminant analysis (DA), which aims to find the linear combination of continuous variables that best discriminates between prespecified, well-defined groups (Legendre and Legendre 1998; McGarigal et al. 2000). DA has two main objectives: (*i*) to exhibit optimal separation of groups based on the discriminant functions, which are linear combinations of the input variables (description) and (*ii*) to predict group membership for an entity of unknown origin based on its measured values in these discriminant functions (classification). In practice, the two objectives are often used in conjunction, since once the classification functions are defined, they are then used to classify new entities. However, like most conventional multivariate analyses, DA is based on linear principles, although the majority of variables used in fisheries and environmental sciences (the species composition of sale bills in our case) show nonmonotonic and nonlinear relationships (James and McCulloch 1990; Mann 1993).

A second alternative, which also overcomes the problems inherent to conventional multivariate statistical analyses, is artificial neural networks (ANNs). These sophisticated modelling techniques were initially intended to mimic the functioning of the human brain (Stern 1996). ANNs manage large, complex data sets well and are especially suitable when relationships between variables are nonlinear or even unknown (Lek et al. 1996). ANNs are based on the same learning processes as the animal brain, which gathers information from the environment (input data) and gives an answer (output data) after using learned training algorithms. This approach circumvents the major problems of the conventional methodologies described above because uncertainty is possible for group membership in the training data set (an entity can belong to more than one category), the method is data-driven (no explicit relationship is assumed to exist between sale bills and FTs), and the ANN parameterization is based exclusively on maximizing the performance of predictions. ANNs have been successfully applied across a broad range of scientific domains (see Lek and Guégan 1999), which demonstrates that they perform better than more classical modelling methods in many cases.

Table 1. Total number of daily samplings on board commercial trawlers off Mallorca (Balearic Islands, western Mediterranean) during 2001–2006 and the corresponding fishing tactics performed in each daily fishing trip.

Fishing tactic(s)	2001	2002	2003	2004	2005	2006	Total
SS	5	10	8	7	11	11	52
DS	4	7	3	6	7	9	36
US	1	2	3	3	1	—	10
MS	18	22	20	22	11	13	106
SS + DS	6	6	2	4	4	2	24
SS + US	4	4	4	13	1	4	30
SS + MS	4	3	5	7	5	4	28
DS + US	1	—	2	4	2	1	10
DS + MS	—	—	2	2	2	1	7
US + MS	1	—	1	3	4	4	13
SS + DS + US	1	—	—	—	—	—	1
SS + US + MS	1	—	1	1	1	1	5
DS + US + MS	—	—	1	—	—	—	1
Total	46	54	52	72	49	50	323

Note: These different fishing tactics are defined depending on the bathymetric strata exploited: SS, shallow shelf; DS, deep shelf; US, upper slope; MS, middle slope.

In this paper, both DA and ANN approaches are used with large amounts of daily landing data to infer the FTs employed by commercial boats. The information obtained by onboard observers, who registered the FTs actually performed on the fishing trip, was used to assign the sale bills to their corresponding FTs. This allowed us to validate the reliability of the two methodological approaches. To improve trawl fishery management in multifleet and multispecific fisheries, like the Mediterranean ones, it is of utmost importance to identify the FTs that are actually used. The complexity of these fisheries may lead to misinterpretations about the relative abundance of specific stocks if CPUE estimates are not analyzed considering homogeneous fishing practices.

Materials and methods

Data from 323 daily samplings onboard commercial trawlers off Mallorca (Balearic Islands, western Mediterranean) were taken from 2001 to 2006 (Table 1). During each daily sampling, a single or several (up to three) hauls were performed, which amounted to a total of 516 individual hauls. Since these data come from a project directed at surveying the trawl fleet in the area, the uneven distribution of the FTs analyzed reflects the fishing strategies actually used but prevents having a suitable, balanced sampling design. The onboard observer recorded both the FT performed and the catch composition according to species for each individual haul. The use of three different FTs was only observed in seven cases; therefore, these cases were removed from the discriminant and neural network analyses. Finally, the daily sale bills corresponding to the 316 sampled days with less than three different FTs were obtained from the central fish auction wharf of Mallorca. These daily landings by species or commercial categories per vessel, along with the FTs actually performed obtained from the onboard program, were used to carry out the discriminant and neural network analyses.

A priori defined FTs

Previous studies, carried out using sampling on board trawlers under commercial conditions, have detected four different FTs in the bottom trawl fishery off Mallorca (Guijarro and Massutí 2006; Ordines et al. 2006). These four strategies are related to the exploitation of different bathymetric strata on the continental shelf (where the target species are fishes and cephalopods) and slope (where the fleet targets crustaceans). The target species and the depth range exploited in these four FTs are the following: (*i*) shallow shelf (SS) (40–80 m): *Spicara smaris*, *Mullus surmuletus*, *Octopus vulgaris*, and a mixed-fish category; (*ii*) deep shelf (DS) (125–235 m): *Zeus faber*, *Mullus surmuletus*, *Merluccius merluccius*, and a mixed-fish category composed of species different from those of the category of the same name for the SS; (*iii*) upper slope (US) (350–600 m): targeting *Nephrops norvegicus* but with an important bycatch of *Merluccius merluccius*, *Lepidorhombus boscii*, and *Micromesistius poutassou*; and (*iv*) middle slope (MS) (600–750 m): the only target species is *Aristeus antennatus*, which is taken along with a bycatch that includes *Galeus melastomus*, *Phycis blennoides*, and *Geryon longipes*.

A preliminary analysis was conducted to corroborate whether our onboard samplings were representative of these FTs. The data collected during the 516 individual hauls, which corresponded to the 323 daily onboard samplings, were used to build up a matrix containing the biomass (kilograms) per haul of the commercial species that appeared in more than 5% of the hauls. To factor out variations not directly related to the FT used (i.e., particular characteristics of the boats, gears, fishermen's skills, etc.), the data were previously standardized by dividing the biomass of each species by the total biomass in each haul. A cluster analysis was then performed on this data matrix using the Bray–Curtis coefficient (Bray and Curtis 1957) and the unweighted pair-group method with arithmetic mean (UPGMA). The Bray–Curtis coefficient was chosen because it calculates the similarity between two samples and

only takes into account the species that are present in at least one of the two samples (Clarke and Warwick 1994), which is especially suitable in our case owing to the high number of double zeros in the data matrix. Finally, the similarity percentage analysis (SIMPER) was used to (*i*) calculate the average similarity within, and dissimilarity between, the groups resulting from the cluster analysis and (*ii*) determine the contribution of the most important species to this average similarity in each cluster. Both the cluster and the SIMPER analyses were carried out using PRIMER (Clarke and Gorley 2006).

Raw data and noise filtering

A total of 81 commercial categories (named species thereafter) were present in the daily sale bills corresponding to the 323 onboard samplings. Filtering was applied to eliminate noise from the sale bills data. In a first step, occasional species (prevalence <5% in the samples) were excluded from the analysis, as they represent unusual catches or bycatch species that only become valuable landings in some fishing trips. In addition, fish mixtures that were composed of different species but known by the same commercial name were also removed. This is the case of the mixed-fish category for the shallow and deep shelf; these two mixtures have a well-differentiated species composition but are referred to by the same name on the sale bills. As a result of this filter, the data matrix was reduced to 33 species. However, as the results of the ANNs using these 33 entries were not as successful as expected in terms of correctly classified instances, a second noise filtering strategy that consisted of retaining the first few axes resulting from a correspondence analysis (CA) was also applied. CA (Benzécri et al. 1973; Legendre and Legendre 1998; ter Braak and Smilauer 2002) is a dimension reduction technique that generates a new space having one fewer dimension than the original one but where the new axes are ordered according to the variance explained. The position of each sale bill in the original space is defined by the biomass of the species it contains. The between-sample similarities in the new space are interpreted in terms of the relative biomasses of the original data. To determine the number of axes to be retained, several trials were carried out in which both DA and ANNs were run using an increasing number of axes (from 2 to 10). Finally, a cluster analysis using the first axes resulting from this previous CA as entries was applied to show the performance of this multivariate technique in the classification of FTs. In this case, the cluster analysis was carried out using the Euclidean distance and the UPGMA.

Performance of discriminant analysis and artificial neural networks

Discriminant analysis

DA is a linear modelling method that determines the linear combinations of variables (discriminant functions) that best discriminate between predefined groups (Legendre and Legendre 1998). Observations are placed in a new space (discriminant space), which has $n - 1$ axes or discriminant functions, with the constraint of maximizing the differences between groups. DA automatically computes the classification functions, which should not be confused with the discriminant functions. There are as many classification functions as there are groups and they can be used to determine to which group each new case is most likely to belong. DA is a suitable multivariate technique to apply in our case because we have a priori well-defined FTs that we first want to characterize with the classification functions and then use these functions to assign daily sale bills to unknown FTs. In this analysis, 10 classification functions were calculated, which corresponded to the four single FTs and the six combinations of two FTs observed during the study period (Table 1).

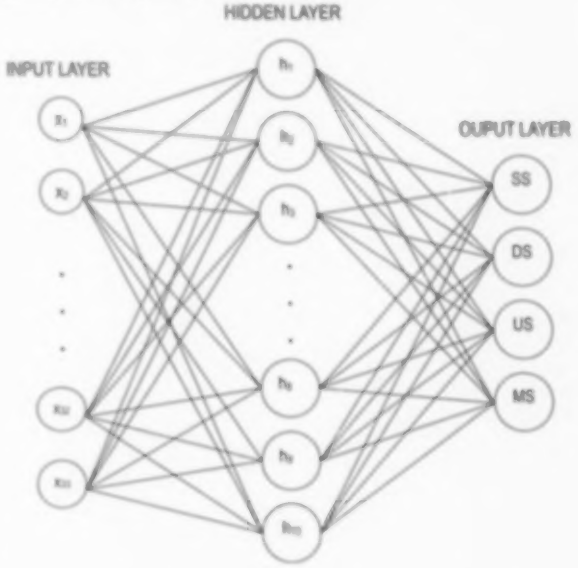
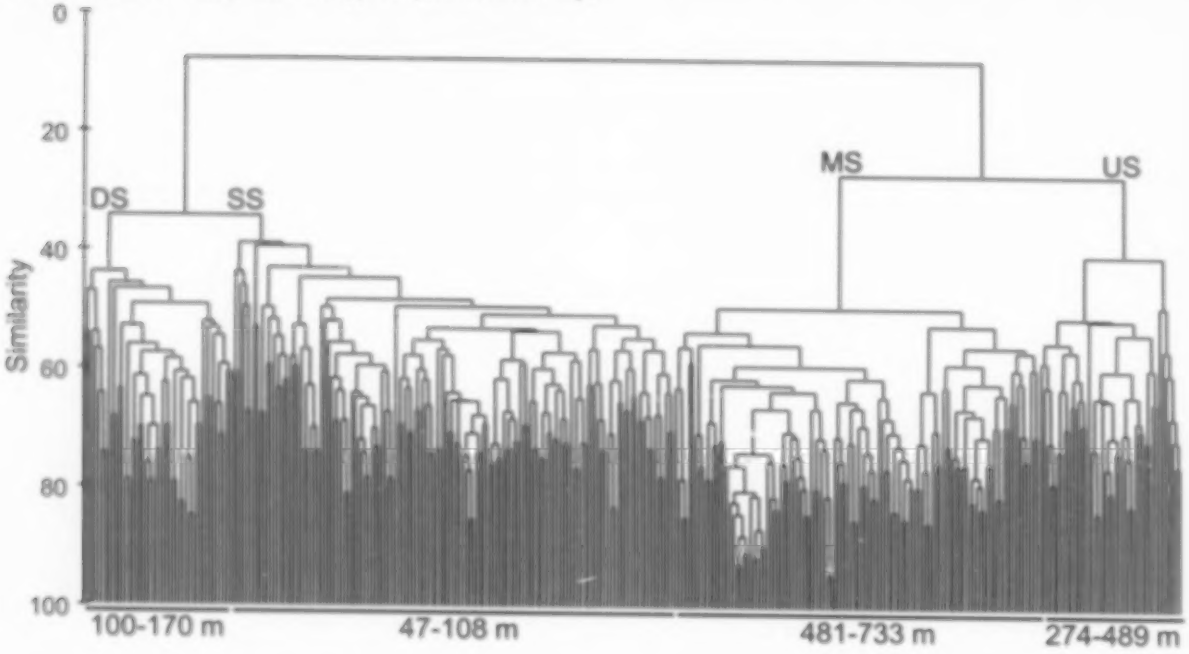


Fig. 1. Architecture of one type of artificial neural network used in the present study. The scheme represents a three-layered multilayer perceptron with 10 neurons in the hidden layer and 33 neurons in the input layer corresponding to the 33 commercial species in the daily sale bills of trawlers from Mallorca (Balearic Islands, western Mediterranean) sampled from 2001 to 2006. The output layer represents the four different fishing tactics actually employed by the trawling fleet in the study area (shallow shelf (SS), deep shelf (DS), upper slope (US), and middle slope (MS)). Neurons from one layer are interconnected to all neurons of neighbouring layers, but no connections are established within a layer or feedback connection. The values of the output neurons were encoded using a fuzzy approach in which the sum of the membership values of the four fishing tactics equals 1 for each output.

Artificial neural networks

There are many different types of ANNs, which are classified according to their learning process and learning algorithm. ANNs accept both categorical and quantitative variables to perform classification and regression tasks, respectively. However, some variables can be treated as either categorical or quantitative, and consequently, most regression algorithms can also be used for classification by encoding categorical target values (Sarle 1997). In the present paper, two types of supervised feed-forward ANNs were used: (*i*) the multilayer perceptron (MLP) with a softmax ac-

Fig. 2. Cluster obtained using the 516 individual hauls carried out in 323 daily fishing trips analyzed during the sampling on board of commercial trawlers off Mallorca (Balearic Islands, western Mediterranean) between 2001 and 2006. The resulting groups, which are shown with their corresponding bathymetric range, reflect the different fishing tactics described in previous studies carried out in the area. SS, shallow shelf; DS, deep shelf; US, upper slope; MS, middle slope.



tivation function and (*ii*) the generalized regression neural network (GRNN). The architecture of a three-layered MLP is defined by highly interconnected neurons (units or nodes) that process information in parallel along three successive layers (Fig. 1). The input layer contains as many neurons as independent variables or descriptors used to predict the dependent variables, which in turn constitute the output layer. In our case, the input layer is constituted by the 33 species present in the sale bills or the first axes from a previous CA, while the output layer has four neurons corresponding to the four individual FTs. The third layer, called the hidden layer, is situated between the input and output layers and its number of layers and (or) neurons is an important parameter, since it optimizes the performance of the ANN. Neurons from one layer are interconnected to all neurons of neighbouring layers, but no connections are established within a layer or feedback connection. To determine which structure performs best with our data, the number of neurons in the hidden layer of the MLP was allowed to vary from one half to double the number of input neurons (Scardi 2001). This was applied to the raw data, the 33 species present in the sale bills, and the first axes from a previous CA. In the first case, however, steps of 5 nodes from 15 to 65 were used owing to the large number of trials to perform and to the fact that each individual trial was very time consuming. More complex structures such as ANNs with more than one hidden layer were not considered. Unlike MLP, GRNNs do not have the problem of defining the number of neurons in the hidden layer because there is the same number of neurons as there are cases in the training data set. Neurons in GRNNs follow Gaussian (bell-shaped) functions, and the maxima and the shape are the parameters to be optimized (Specht 1991). Training any type of ANN consists of using a training data set to adjust the connection weights to minimize the error between observed and predicted values. Once the connections have been established by training, they remain fixed in the hidden layer and the ANN can be used for testing. After the network has been trained, it should be able to correctly classify patterns that are different from those used during the training phase.

Analysis procedure

To carry out the discriminant and neural network analyses, the raw data (316 daily sale bills with their corresponding FTs) were divided into two different subsets: (*i*) the training set, which was used to determine the classification functions that best describe the different FTs in the DA and which was also used to train the ANN to learn correlated patterns between the species compositions in the bills and the corresponding FTs, and (*ii*) the testing set, a data subset that is independent of the training set and in which only the daily sale bill information is used to analyze the predictive power of both the DA and the ANN. The accuracy, the total fraction of the samples correctly identified, provides a measure of the recognition performance when applied to training sets and a measure of prediction performance when applied to testing sets. In all of the analyses, the training and testing data sets had 266 and 50 units, respectively, both randomly chosen from the total of 316 available units. To minimize the possibility that the estimation of success was biased ow-

Table 2. Results of similarity percentage analysis for the four groups detected in the cluster analysis of individual hauls shown in Fig. 2.

	$\bar{Y}$	$\bar{S}_i$	$\bar{S}_i$/SD	$\%\bar{S}_i$	$\Sigma\%\bar{S}_i$
Shallow shelf, $\bar{S}_iG = 48.56$					
Mullus surmuletus	9.74	6.34	1.74	13.06	13.06
Octopus vulgaris	7.94	6.16	1.52	12.69	25.75
Spicara smaris	13.50	4.89	1.08	10.07	35.81
Scyliorhinus canicula	3.59	3.79	1.14	7.80	43.61
Chelidonichthys lastoviza	2.15	2.84	1.21	5.86	49.47
Raja spp.	3.04	2.81	0.92	5.80	55.26
Serranus cabrilla	2.28	2.75	1.24	5.66	60.93
Trachinus draco	1.49	2.35	1.33	4.84	65.77
Loligo vulgaris	2.51	2.19	0.88	4.50	70.27
Scorpaena scrofa	1.11	1.98	1.20	4.07	74.34
Pagellus erythrinus	2.39	1.79	0.96	3.68	78.03
Deep shelf, $\bar{S}_iG = 50.76$					
Merluccius merluccius	10.44	11.40	2.74	22.46	22.46
Scyliorhinus canicula	2.79	5.47	2.20	10.78	33.25
Trachurus mediterraneus	4.19	2.67	0.69	5.27	38.52
Mullus surmuletus	2.57	2.65	1.14	5.22	43.73
Lophius budegassa	1.11	2.64	1.31	5.20	48.93
Raja spp.	2.68	2.33	0.79	4.59	53.52
Trachinus draco	1.08	2.29	1.32	4.50	58.03
Mullus barbatus	1.08	2.12	1.07	4.18	62.21
Centracanthus cirrus	3.94	2.07	0.54	4.08	66.29
Zeus faber	1.43	2.05	0.85	4.04	70.33
Lepidorhombus boscii	0.91	1.83	0.86	3.60	73.93
Chelidonichthys cuculus	1.34	1.76	0.77	3.46	77.39
Upper shelf, $\bar{S}_iG = 50.91$					
Micromesistius poutassou	9.13	9.38	1.27	18.43	18.43
Merluccius merluccius	4.84	8.86	2.95	17.41	35.84
Parapenaeus longirostris	2.80	4.62	1.25	9.07	44.90
Phycis blennoides	1.83	4.46	1.66	8.75	53.66
Lepidorhombus boscii	1.24	3.93	1.81	7.72	61.37
Scyliorhinus canicula	1.98	2.82	0.83	5.55	66.92
Lophius budegassa	1.07	2.56	1.11	5.03	71.96
Nephrops norvegicus	1.40	2.42	0.73	4.75	76.71
Middle shelf, $\bar{S}_iG = 55.38$					
Aristeus antennatus	7.81	27.40	2.65	49.47	49.47
Phycis blennoides	1.17	6.58	1.46	11.88	61.34
Micromesistius poutassou	1.12	4.82	0.97	8.70	70.04
Merluccius merluccius	0.63	4.79	1.26	8.65	78.69

Note: Species are ordered according to their importance in the average similarity contribution to the within-group average similarity ($\bar{S}_iG$), and only those reaching 75% of $\bar{S}_iG$ are shown. $\bar{Y}$, mean yield (kg/haul); $\bar{S}_i$, species average similarity contribution to $\bar{S}_iG$; $\%\bar{S}_i$, percent contribution to $\bar{S}_iG$; $\Sigma\%\bar{S}_i$, cumulative percent contribution to $\bar{S}_iG$. $\bar{S}_i$/SD (where SD stands for the standard deviation of $\bar{S}_i$) is also shown as an indicator of consistency in the contribution to $\bar{S}_iG$ of a particular species. Higher values of one species compared with another indicate that the first one contributes more consistently to the within-group similarity.

ing to the data selected as training and testing sets, 500 consecutive runs were completed in which both data sets were randomly reassigned to each category. Both the DA and the ANNs were implemented in R scripts (R version 2.5.1, www.r-project.org/) using the MASS (Ripley and Venables 2007), Vegan (Oksanen et al. 2007), neural (Nagy 2008), and gmnR (Arrington 2005) libraries.

In supervised learning, the confusion matrix is used to display the entire set of predicted/observed cases, where the columns represent the instances in a predicted class and the rows represent the instances in an actual class (Provost and Kohavi 1998). To determine the success of both DA and ANNs in predicting FTs, three performance measures were calculated: the Cohen Kappa statistic (Cohen 1960; Titus et al. 1984), the number of correctly classified instances (CCI), and an ad hoc modification of CCI, which we called CCI2.

The Kappa statistic is a useful measure of chance-corrected classification when prior probabilities are estimated according to group sample sizes and is defined as $\text{Kappa} = \left(p_o - \sum_i^G p_i q_i\right) / \left(1 - \sum_i^G p_i q_i\right)$, where G is the number of groups, p_o is the observed frequency of samples that are correctly classified, p_i is the frequency of samples in the ith group, and q_i is the frequency of samples classified into the ith group. A Kappa of 0 indicates no improvement over chance and a Kappa of 1 indicates perfect assignment. CCI is calculated as follows: CCI = 100(TP + TN)/(TP + FP + FN + TN), where TP and FP stand for true- and false-positive predicted cases, respectively, and TN and FN stand for true- and false-negative, respectively. Unlike CCI, where true and false cases were calculated for the entire output of the four neurons, these instances were calculated for each individual value in the four output neurons in CCI2. That is, for a predicted output 1011 corresponding to an observed output 1001 (each of these 1 or 0 values represent correct and incorrect predictions, respectively, in each of the four neurons from the output layer), CCI considers this as a false case, while CCI2 considers there to be three true cases and one false case (predictions).

Results

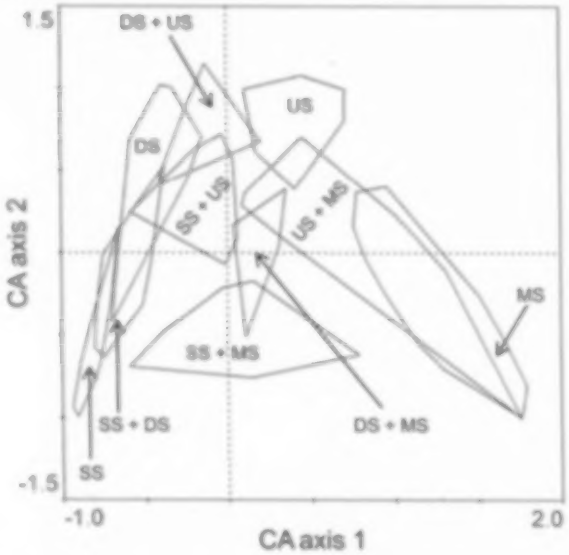
A priori defined FTs

Cluster analysis of the 516 single hauls performed during the onboard sampling resulted in four clear groups that were well differentiated according to depth (Fig. 2). In addition, a SIMPER analysis revealed that these groups were also well differentiated in their species composition, which can be assigned to the four FTs described in previous studies (Table 2): (*i*) SS: between 47 and 108 m depth dominated by *Mullus surmuletus*, *Octopus vulgaris*, and *Spicara smaris*, (*ii*) DS: between 100 and 170 m depth with the highest yields corresponding to *Merluccius merluccius*, (*iii*) US: between 274 m and 489 m depth dominated by *Micromesistius poutassou*, *Merluccius merluccius*, and *Parapenaeus longirostris*, and (*iv*) MS: between 481 and 733 m with the highest yields corresponding to *Aristeus antennatus*. The average dissimilarity between groups was high both for adjacent (SS vs. DS = 65.7, DS vs. US = 74.0, US vs. MS = 73.0) and for nonadjacent (SS vs. US = 87.3, SS vs. MS = 96.8, DS vs. MS = 91.4) strata. Such a clear discrimination is due to single hauls generally being performed on well-delimited bathymetric strata that represent a specific FT, and therefore, overlapping between consecutive strata is not usual.

Raw data and noise filtering

Trials with both DA and ANNs using from 2 to 10 axes from a previous CA showed that the best results were obtained by retaining the first six axes; therefore, these six axes were used as input data in posterior DA and ANN analyses. The scatterplot of the first two CA axes (Fig. 3) showed that, although the discrimination between groups of fishing trips in which a single FT was carried out is clear, there is significant overlapping in the groups of trips where more than one FT was performed. This overlap was also reflected in the cluster obtained using the first six CA axes (Fig. 4). To obtain from this cluster a number of groups similar to the total number of different FTs used (six single FTs plus four combinations), the cutoff value was established at a distance of 1.27, which gave rise to 11 groups. Many of these 11 groups obtained cannot be objectively assigned to FTs, which is demonstrated by the composition of FTs in each group (Table 3). This result confirmed that clustering is not a useful tool for FT classification in multispecific fisheries where two or more FTs may be used during a single fishing trip.

Fig. 3. Biplot of the 316 daily sale bills analyzed during the sampling period represented in the two first correspondence analysis (CA) axes. The CA was carried out to reduce dimensionality in the raw data, which consisted of a matrix of species abundance (33 commercial species) present in the daily sale bills. Samples with the same fishing tactic are represented within polygons for clarity. SS, shallow shelf; DS, deep shelf; US, upper slope, MS, middle slope.



Performance of discriminant analysis and artificial neural networks

The output values obtained in both the classification functions of the DA and the output neurons of the ANNs showed a distribution that was strikingly skewed towards 1 or 0, which corresponded, respectively, to correct and incorrect assignment to a determined FT (Fig. 5). This fact simplified selecting a threshold for inferring the use of a specific FT, which was then established at the 0.5 cutoff value in both methods.

In a first trial, both DA and ANNs (MLP and GRNN) were run using the raw data in the input layer (i.e., the 33 commercial species found in the sale bills). MLP trials were carried out with different numbers of nodes in the hidden layer, from 15 to 65 in steps of 5 nodes. The best results (Fig. 6) were obtained with DA, which showed higher values than the different ANNs used, both in the Kappa statistic and in the CCI and CCI2. The results of the MLP analyses did not show any consistent trend as the number of nodes in the hidden layer increased. Considering ANNs, GRNN ob-

Fig. 4. Cluster analysis performed on the 316 daily sale bills corresponding to the days with an onboard observer during the sampling of commercial trawlers off Mallorca (Balearic Islands, western Mediterranean) between 2001 and 2006. This analysis was carried out by calculating a Euclidean distance matrix from the first six axes obtained in a previous correspondence analysis (see Fig. 2) and then applying UPGMA. Table 3 shows the composition of the 11 groups obtained.

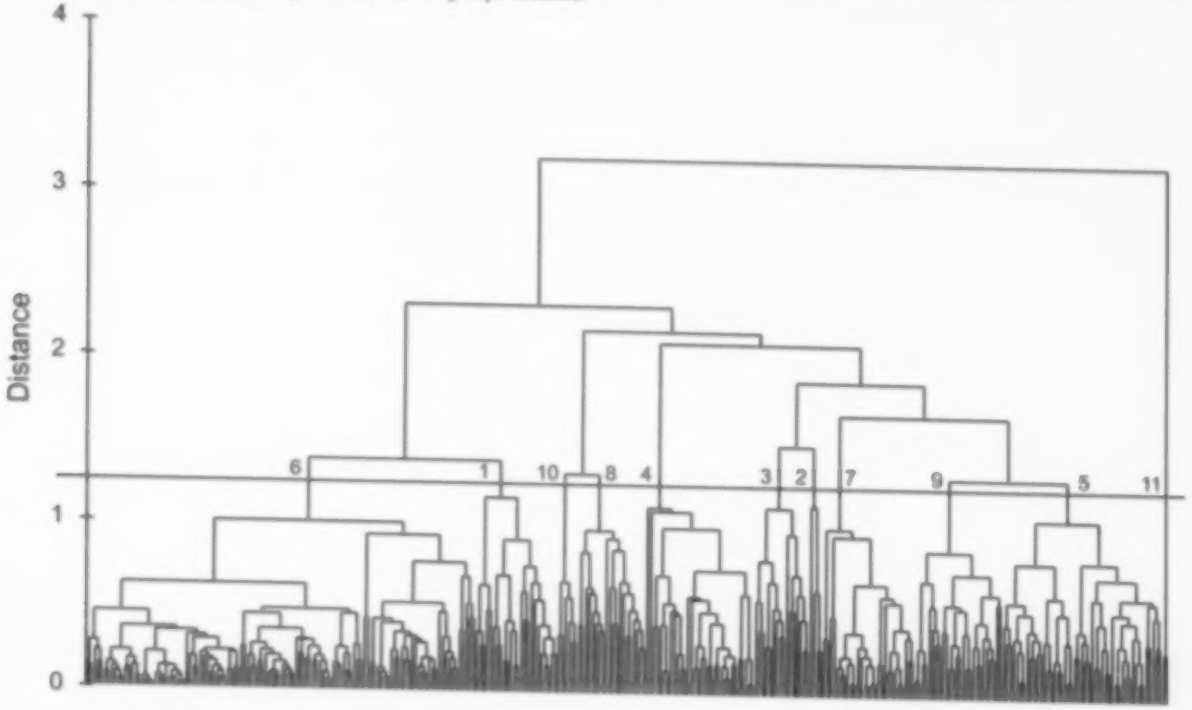


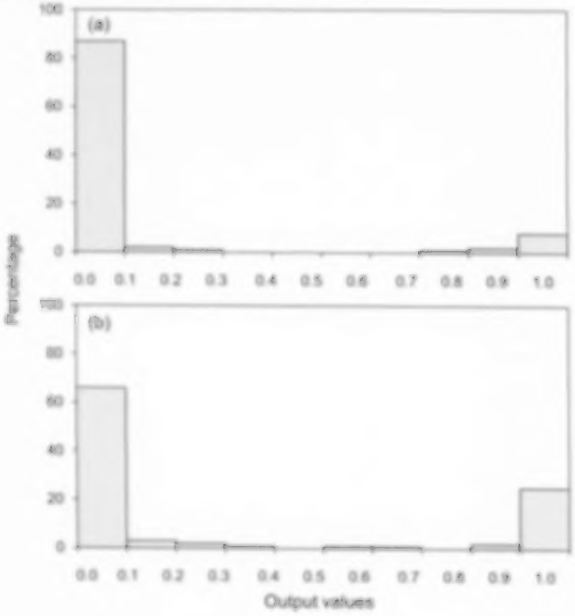
Table 3. Composition, in terms of percentage of fishing tactics, of the 11 groups obtained in the cluster analysis shown in Fig. 4, which was performed using the information from the 323 daily sale bills corresponding to the onboard sampling carried out in Mallorca (Balearic Islands, western Mediterranean) during 2001–2006.

	Cluster No.										
Observed fishing tactic(s)	1	2	3	4	5	6	7	8	9	10	11
SS	—	—	—	3.1	44.7	—	88.9	—	16.7	—	100.0
DS	—	—	12.5	90.6	10.6	—	—	—	—	—	—
US	—	—	—	—	—	—	—	35.0	—	40.0	—
MS	—	—	—	—	—	92.4	—	—	—	20.0	—
SS + DS	—	—	12.5	—	40.4	—	3.7	—	4.2	—	—
SS + US	—	—	37.5	—	—	—	—	50.0	41.7	20.0	—
SS + MS	72.7	—	—	—	2.1	—	7.4	—	37.5	—	—
DS + US	—	100.0	18.8	6.3	—	—	—	5.0	—	20.0	—
DS + MS	27.3	—	—	—	2.1	—	—	—	—	—	—
US + MS	—	—	18.8	—	—	7.6	—	10.0	—	—	—
No. of samples	24	4	16	32	47	119	27	20	26	6	2

Note: SS, shallow shelf; DS, deep shelf; US, upper slope; MS, middle slope. For purposes of clarity, zero values have been replaced by a dash.

tained by far the worst results, with the Kappa statistic as low as 0.093. To try to improve these results, both DA and ANNs were fed with the six axes from a previous CA as input neurons. In the MLP analyses, the number of nodes in the hidden layer was allowed to vary from 3 to 12. In this new trial, all of the methods improved their results; the Kappa statistic for the DA increased by 14%, whereas the MLPs reached values ranging from 0.64 to 0.73 compared with the 0.60–0.62 obtained using the raw data. In this case, the results of MLP analyses improved as the number of neu-

Fig. 5. Examples of frequency of output values in (*a*) the discriminant analysis and (*b*) the generalized regression neural network, one type of artificial neural network used in this study. These output values showed a distribution that was very skewed towards 1 or 0 in both approaches, corresponding, respectively, to correct and incorrect assignment to a determined fishing tactic. Based on these results, the threshold for assuming the use of a specific tactic was established at the 0.5 cutoff value in both methods.



rons in the hidden layer increased and reached an asymptotic value of about 0.72 in the Kappa statistic with eight nodes. However, the most remarkable case was the GRNN, as its Kappa statistic increased by approximately 700%, reaching results that are comparable with those obtained using DA. Both methods showed a Kappa statistic and CCI of 0.74 and 79%, respectively, and a CCI2 higher than 93%.

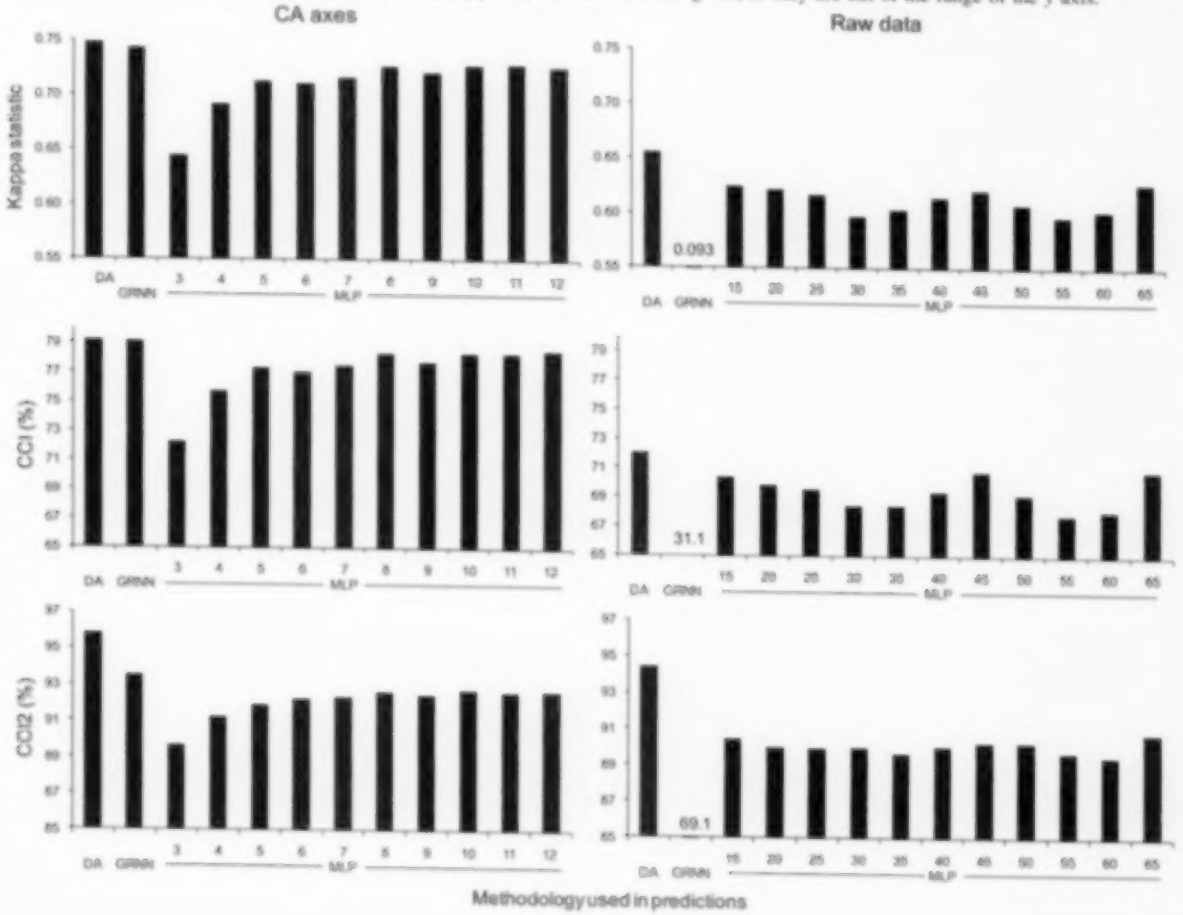
The confusion matrix is only displayed for the two methods showing the best results, the DA (Table 4) and the GRNN (Table 5) both fed with the six axes from a previous CA. There was a large difference between the two methods in the number of outputs for which no clear prediction was obtained (in the case of DA) or for which the predicted FT was not actually present in the input data set (in the case of GRNN), since this was negligible in the GRNN (0.04% of total cases) but reached 2% in the DA. With the exception of the predictions corresponding to the US made by the GRNN, which was only successful in 26% of the cases, the two methods were generally quite successful in predicting individual FTs, ranging between 76% and 96% success. Taking into account the predictions of multiple FTs, the worst results were obtained in the combinations of adjacent depth strata. In this sense, the most problematic case was found in the combination of FTs performed on the slope (US + MS), which gave percentages lower than 22% in both methods, followed by the DS + US case (35% in GRNN and 53% in DA). In these last two cases, significant percentages were assigned to the single FTs that constituted the combined tactic and this was especially evident in the US + MS case where 44%–63% of the predictions were misclassified as MS. The success percentages in the two adjacent strata from the continental shelf (SS + DS) were also rather low (47% in GRNN and 68% in DA) compared with those obtained in nonadjacent strata.

Discussion

Fishery scientists use CPUE data as an indicator of population abundance whenever the assumption of uniform fishing effort is accomplished (Hilborn and Walters 1992). However, this rarely occurs in the real world because effort shows significant spatiotemporal variations, especially in multigear and multispecies fisheries where fishermen may carry out different FTs even during a single day. In this context, using data on commercial landings to infer stock abundances depends on methods directed at identifying the FTs actually performed, and hence the effective fishing effort, from the mixture of species present in the catch composition. Up to now, this identification has been performed using multivariate techniques, such as clustering or dimension reduction analyses (e.g., discriminant, principal components, or correspondence analyses). In all cases, as authors did not have information on the fishing strategies actually performed by fishermen, the groups resulting from these analyses were subsequently assigned to different FTs based on the species composition of each group (Silva et al. 2002; Jiménez et al. 2004; Fall et al. 2006). For the present paper, the FTs actually employed in the different individual hauls of the commercial trawlers in daily fishing trips were known, as they had been recorded by onboard observers. The daily sale bills corresponding to all of these samplings were obtained afterwards, and therefore, we also had the information on catch composition (species or commercial category) along with the FTs actually performed to take this catch. This precludes the assignment to "artificial" or nonobserved FTs, as occurs in many cases as a result of the a posteriori grouping criteria applied in previous studies using classical multivariate approaches.

Contrary to scientific surveys, which in most cases are snapshots of particular spatiotemporal situations, daily sale bills from fishery data constitute powerful tools for analyzing stock abundances, since they allow the overall resources (information is available for the entire fleet) to be followed all year round with a finer (daily) time scale. In this work, the performance of two analytical tools, DA and ANNs, in predicting FTs from the species composition in daily sale bills was determined. Although DA was widely used as a classification technique in the ecological and environmental sciences in the 1980s (e.g., Van Horne and Ford 1982; Williams 1983; Titus et al. 1984), the first applications of ANNs did not appear until the early 1990s after the publication of the error backpropagation algorithm (Rumelhart et al. 1986). Since then, it has been used increasingly in a wide range of fields (Lek and Guégan 1999). Many of the published works on ANNs in marine and freshwater ecology compare this modelling method with classical multivariate statistical procedures, such as multiple linear regression (e.g., Laë et al. 1999; Scardi and Harding 1999; Ibarra et al.

Fig. 6. Performance of discriminant analysis (DA) and two different types of artificial neural networks, a multilayer perceptron (MLP) and a generalized regression neural network (GRNN), in predicting fishing tactics employed by commercial trawlers off Mallorca (Balearic Islands, western Mediterranean). Trials were carried out using the raw data (the 33 species in the daily sale bills) and the first six axes from a previous correspondence analysis (CA) in the input data set. Numbers on the *x* axis refer to the number of nodes in the hidden layer of MLPs. For each trial, the Kappa statistic, the number of correctly classified instances (CCI), and an ad hoc defined CCI2 (see Materials and methods) are shown. Values corresponding to GRNN applied to the raw data are given, as they are out of the range of the *y* axis.



2003) or DA (e.g., Engelhard et al. 2003; Maravelias et al. 2003; Engelhard and Heino 2004). However, no definitive conclusions can be extracted from these works because, while many of them found that ANNs clearly performed better than the classical techniques (e.g., Laë et al. 1999; Scardi and Harding 1999; Ibarra et al. 2003), others obtained similar results with the different approaches used (e.g., Haralabous and Georgakarakos 1996; Engelhard et al. 2003; Engelhard and Heino 2004). In spite of this, and provided that enough information is available, it is not possible that a multiple regression outperforms an ANN because if a process is inherently linear, an ANN is as effective as a linear model, although it may take more data to be properly generalized. When ANNs were not found to perform better than linear methods, it was most probably due to nonoptimal training strategies, ANN architectures, or data-limited situations.

Two different types of supervised feed-forward neural networks, a three-layered MLP and a GRNN, were used in the present paper. Although MLP with backpropagation algorithm is one of the most frequently used ANNs in environmental sciences (Lek and Guégan 1999), GRNN has been scarcely applied. To our knowledge, only Foody and Cutler (2006) have used this type of ANN in a work comparing the performance of both MLP and GRNN to map the species richness and composition of tropical forests, obtaining that the most accurate predictions were derived from the GRNN. In spite that, in theory, ANNs manage well with large sets of input data, our results improved when the raw data entries (33 species present in the sale bills) were replaced by the first axes from a previous CA. This improvement was observed in all three methods (DA, MLP, and GRNN), but it was especially significant in the case of the GRNN, which then became, along with DA, one of the two

Table 4. Confusion matrix of a discriminant analysis for predicting fishing tactics performed by commercial trawlers off Mallorca (Balearic Islands, western Mediterranean) during 2001–2006.

Observed fishing tactic(s)	Predicted fishing tactic(s)										
	SS	DS	US	MS	SS + DS	SS + US	SS + MS	DS + US	DS + MS	US + MS	Others
SS	**3194 (70)**	72 (2)	15 (0)	—	726 (17)	41 (1)	41 (1)	—	—	—	87 (2)
DS	1 (0)	**2337 (81)**	—	—	401 (14)	—	—	146 (5)	—	—	1 (0)
US	—	—	**655 (80)**	—	—	35 (4)	—	43 (5)	—	43 (5)	39 (5)
MS	—	—	100 (1)	**8019 (96)**	—	—	—	—	—	188 (2)	47 (0)
SS + DS	410 (22)	—	—	—	**1291 (68)**	13 (1)	1 (0)	138 (7)	—	—	41 (2)
SS + US	—	—	226 (10)	—	235 (10)	**1648 (73)**	70 (3)	7 (0)	—	—	71 (3)
SS + MS	124 (6)	—	—	245 (11)	49 (2)	—	**1663 (76)**	—	—	—	104 (5)
DS + US	—	174 (21)	162 (19)	—	4 (0)	43 (5)	—	**442 (53)**	—	—	11 (1)
DS + MS	—	13 (2)	—	—	77 (14)	—	74 (13)	—	**382 (69)**	—	6 (1)
US + MS	—	—	163 (16)	456 (44)	—	14 (1)	—	72 (7)	75 (7)	**177 (17)**	88 (8)

Note: Inputs were the first six axes from a previous correspondence analysis performed with the 33 species in the daily sale bills. The training data set in the discriminant analysis (see Materials and methods) contained the 10 groups shown in the table, which correspond to the four single fishing tactics and the six different combinations of two fishing tactics observed throughout the sampling. Values are absolute numbers of instances (and percentages in parentheses) out of 25 000 trials in which the number of cases (50) in the training and testing sets were randomly chosen 500 consecutive times. SS, shallow shelf; DS, deep shelf; US, upper slope; MS, middle slope; Others, predictions that DA was not able to classify among the observed groups. For purposes of clarity, the values on the diagonal are in bold.

Table 5. Confusion matrix of a generalized regression neural network for predicting fishing tactics performed by commercial trawlers off Mallorca (Balearic Islands, western Mediterranean) during 2001–2006.

Observed fishing tactic(s)	Predicted fishing tactic(s)										
	SS	DS	US	MS	SS + DS	SS + US	SS + MS	DS + US	DS + MS	US + MS	Others
SS	**3541 (86)**	140 (3)	—	—	363 (9)	—	64 (2)	—	—	—	—
DS	36 (1)	**2293 (82)**	—	—	331 (12)	—	2 (0)	125 (4)	9 (0)	1 (0)	—
US	—	—	**212 (26)**	113 (14)	—	282 (35)	—	24 (3)	—	183 (22)	—
MS	—	—	81 (1)	**8043 (96)**	—	—	25 (0)	8 (0)	2 (0)	200 (2)	—
SS + DS	475 (24)	347 (18)	—	—	**911 (47)**	64 (3)	114 (6)	7 (0)	15 (1)	—	2 (0)
SS + US	11 (0)	—	181 (8)	11 (0)	31 (1)	**2012 (85)**	62 (3)	24 (1)	2 (0)	40 (2)	5 (0)
SS + MS	92 (4)	1 (0)	—	93 (4)	86 (4)	11 (0)	**1946 (86)**	—	24 (1)	1 (0)	—
DS + US	—	230 (30)	133 (17)	4 (0)	10 (1)	107 (14)	—	**268 (35)**	—	14 (2)	3 (0)
DS + MS	—	14 (3)	—	17 (3)	35 (6)	1 (0)	94 (17)	—	**336 (61)**	50 (9)	—
US + MS	—	1 (0)	52 (5)	652 (63)	—	62 (6)	2 (0)	2 (0)	46 (4)	**221 (21)**	—

Note: In this analysis, the input layer (see Materials and methods) contained six neurons that corresponded to the first six axes from a previous correspondence analysis, while the output layer contained the four single fishing tactics observed throughout the sampling. Values are absolute numbers of instances (and percentages in parentheses) out of 25 000 trials in which the number of cases (50) in the training and testing sets were randomly chosen 500 consecutive times. SS, shallow shelf; DS, deep shelf; US, upper slope; MS, middle slope; Others, predictions containing more than two single fishing tactics not actually observed. For purposes of clarity, the values on the diagonal are in bold.

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approaches showing the highest prediction capacity. This result was unexpected because a typical regression method (i.e., GRNN, outperformed a typical classification method, i.e., MLP). However, using regression algorithms for classification purposes is feasible provided that the target values are encoded as categorical variables (Sarle 1997). In the end, DA and GRNN fed with the axes from a previous CA achieved similar results because in spite that DA (Kappa = 0.75, CCI2 = 95.8) performed slightly better than GRNN (Kappa = 0.74, CCI2 = 93.5), the difference was minimal. Haralabous and Georgakarakos (1996) reported that comparing ANNs and DA is not straightforward because an ANN can only be tested on a subset of training-free cases, while DA can be acceptably tested on the whole data set. However, this is not exactly correct because the performance of DA cannot be tested without an independent test set. The accuracy of DA can be inferred according to the underlying statistics, but these inferences rely on several assumptions that are probably not met in real-world applications (e.g., multinormality). Consequently, a proper comparison should take a single subset of the data to train the ANN and DA and then a separate subset to test both methods. However, this would require having a sufficiently large total number of cases to obtain enough examples in each subset, which is not usual in environmental sciences where sampling programs are costly.

In fact, the dependence of the results on the sample size is reflected in our case, since the success of both DA and GRNN in predicting FTs containing more than 25 cases ranged between 73% and 96% (in CCI values) but decreased significantly for those FTs with lower sample sizes. Along with sample size, the dissimilarity between the species composition of different FTs also plays an important role in interpreting the results because higher dissimilarity between individual FTs implies higher success in identifying mixtures of them. Owing to the continuous substitution of species with depth rather than discrete assemblages separated by distinct boundaries, there is significant overlapping of species in adjacent strata and this is reflected in the catch composition present in the sale bills. This prevents a clear discrimination between successive FTs. In this sense, the similarity percentage analysis showed that the average dissimilarity between adjacent strata was 66%–74%, whereas it increased to 87%–97% between nonadjacent strata. Accordingly, the ranges of successful predictions for DA and GRNN were 17%–68% and 61%–86% for adjacent and nonadjacent strata, respectively. Overlapping and balancing in data are especially important in classification problems (Wythoff 1993; Al-Hadldad et al. 2000) and our results were most probably affected negatively by both shortcomings. The unbalanced sample sizes of our data are evident but this has a straightforward solution for future studies provided they are able to obtain a balanced sampling. In contrast, the problem of overlapping does not have such an easy solution because it is inherent to the data that we are dealing with. Solutions could be focused on reducing this overlapping by means of analytical approaches such as the multivariate technique used in this work. Applying a CA gave better results than using the raw data and future analyses using more efficient tools to reduce overlapping might even improve these results further. Moreover, we would like to point out an important issue inherent to the use of MLPs but not to GRNNs. In most situations, there is no way to determine the best number of hidden nodes (or even the number of hidden layers) without training several networks. To find the best-performing structure, scientists use a series of rules of thumb (Sarle 1997; Scardi 2001), as we did in this study, in which the number of nodes is allowed to vary from one half to double the number of input neurons. This implies that a better structure might be found if trials are performed using a range of values. In our case, we did not try the entire range but used steps of five nodes owing to the large number of trials necessary and the time required to run each one, which in most cases lasted overnight. To improve this drawback in MLPs, there needs to be improvements in the methodologies for determining the best MLP structure (Sarle 1997) and improved computing power to reduce the computing time.

To conclude, assessing mixed fisheries involves a number of complexities, such as the fact that species caught together may have very different status in relation to safe biological limits depending on their population turnover rates. In many cases, this leads to management conflict between ecological and economic objectives (Jennings et al. 1999; Pope et al. 2000; Rätz et al. 2007). Currently, there is general agreement that quota allocations based on single-species considerations fail to curtail the exploitation of demersal stocks to reach sustainable levels (Cotter et al. 2002; Daan et al. 2005). This highlights a need for fleet-specific effort regulations to avoid high discarding rates and unallocated landings (Shepherd 2001; Vinther et al. 2004). In this sense, the analytical approaches proposed here will improve CPUE estimates in mixed fisheries and will contribute to understanding the complex relationships between the fleet and the resources, which are potentially mediated by the local abundance of the resources and market preferences.

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Climate and intraspecific competition control the growth and life history of juvenile sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska

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Abstract: Recent climate changes have had marked effects on the ice-free season and thermal conditions in many high-latitude lakes, but their ecological effects combine with density-dependent processes to affect fish growth and life history. To better understand the relative roles of climate and intraspecific density, we applied Gaussian state–space models to long-term data (1962–2006) on growth of juvenile sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska, USA. Both temperature and density influenced fry size at the end of their first growing season, but the positive effect of temperature exceeded the negative effects of density. Fry growth was affected by the magnitude of their own cohort more strongly than by the previous brood (i.e., yearlings). In contrast, density was more important than temperature in Lake Aleknagik, also in Bristol Bay, over the same period of record, probably because Iliamna Lake is cooler and has generally lower densities of juvenile sockeye salmon than Lake Aleknagik. In both lakes, the size of the fish at the end of the first growing season affects smolt size and age at seaward migration, hence survival at sea and age at maturity, so the relative effects of climate and density depend on the ecological context.

Résumé : Les changements climatiques récents ont eu des effets marqués sur la saison libre de glace et les conditions thermiques dans plusieurs lacs de haute latitude, mais leurs effets écologiques s'allient aux processus dépendants de la densité pour affecter la croissance et le cycle biologique des poissons. Afin de mieux comprendre les rôles respectifs du climat et de la densité intraspécifique, nous avons utilisé des modèles état-espace gaussiens avec des données récoltées pendant une longue période (1962–2006) sur la croissance des jeunes saumons rouges, *Oncorhynchus nerka*, au lac Iliamna, Alaska, É.-U. La température et la densité affectent toutes deux la taille des alevins à la fin de leur première saison de croissance, mais les effets positifs de la température surpassent les effets négatifs de la densité. La croissance des alevins est affectée plus fortement par l'importance de leur propre cohorte que par la cohorte précédente (saumons d'un an). En revanche, la densité est plus importante au lac Aleknagik, de même que dans la baie de Bristol, durant la même période d'inventaire, probablement parce que le lac Iliamna est plus frais et contient généralement des densités plus faibles de jeunes saumons que le lac Aleknagik. Dans les deux lacs, la taille des poissons à la fin de leur première saison de croissance affecte la taille des saumoneaux et l'âge de la migration vers la mer, et donc la survie en mer et l'âge à la maturité; ainsi, les effets respectifs du climat et de la densité dépendent du contexte écologique.

[Traduit par la Rédaction]

Introduction

High-latitude lake systems are characterized by pronounced seasonal cycles of resource availability and scarcity, and evidence for warming and the ecological impacts of climate variability are often pronounced (Magnuson et al. 2000; Root et al. 2003; Berteaux et al. 2004). Lake systems in the Northern Hemisphere have experienced substantial changes in ice cover and phenology, air and water temperatures, evaporation, thermal stratification, and other important limnological events reflecting trends in warmer winters and earlier springs (Schindler et al. 1990; Winder and Schindler 2004; Schindler et al. 2005).

Salmonid fishes (char, trout, and salmon) are often numerically and ecologically important in northern aquatic ecosystems, and their complex life cycles offer insights into the effects of changing climate on life history and ecology. Salmon catch records showed a positive correlation with climate indices across the North Pacific (Beamish and Bouillon 1993) and fit particularly well with phases of the Pacific Decadal Oscillation (PDO) for Alaskan stocks of salmon (Mantua et al. 1997). Studies using paleolimnology have revealed that fluctuations in Pacific salmon populations correlated with changes in climate regimes over several centuries (Finney et al. 2000). Sockeye salmon (*Oncorhynchus nerka*) often spawn at high densities in lakes and tributary streams during the late summer and fall, and the fry emerge the following spring. The juveniles typically rear in lakes for 1 or 2 years, then migrate to the ocean to grow for an additional 1, 2, or 3 years before returning to spawn (Burgner 1991; Quinn 2005). The lacustrine juvenile phase makes them particularly amenable for studies on the effects of changing cli-

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mate because size at the end of the first growing season affects the age and date of seaward migration. Within populations, larger members of a year class tend to migrate a year earlier than smaller members, and larger individuals tend to migrate earlier in the spring than smaller members of their cohort (Foerster 1968; Burgner 1987; Quinn et al. 2009). Size and timing of seaward migration influence marine survival and thus play important roles in overall population productivity (Henderson and Cass 1991; Koenings et al. 1993).

Growth of juvenile sockeye salmon in lakes is positively related to temperature (warmer water increases the physiological scope for growth of sockeye salmon up to about 15 °C; Brett 1995), but growth is also affected by nutrient concentrations, zooplankton quantity and quality, and the density of conspecifics (Hyatt and Stockner 1985; Edmundson and Mazumder 2001; Schindler et al. 2005). However, the relative importance of these factors varies among lakes and among years within a given lake (Burgner et al. 1969; Burgner 1987). Moreover, in systems with two age classes of juveniles rearing in the lake at the same time, there is competition among year classes as well as competition within each year class (Selifonov 1970; Burgner 1987). Climate and density affect growth and thus size at the end of the first growing season in sockeye salmon through direct effects on scope for growth and competition for food (Burgner et al. 1969; Burgner 1987; Schindler et al. 2005). Changes in air temperature can also profoundly affect complex limnological processes such as ice breakup, absorption of solar radiation, and thermal stratification, which influence the timing and rate of production and abundance of phytoplankton and zooplankton (Straile 2000; Scheffer et al. 2001; Winder and Schindler 2004). Understanding the interactions among these factors is important for both explaining historical patterns in life history and survival and also for projecting the effects of future climate change on the populations.

In this study we used long-term data (1962–2006) on juvenile sockeye salmon in Iliamna Lake in the Bristol Bay region of southwestern Alaska to determine the relative roles of climate and density in controlling growth and the life history transition to the smolt stage. The Iliamna Lake populations of sockeye salmon include fish that migrate to sea after either one or two full growing seasons in the lake, allowing us to study competitive interactions between year classes. Iliamna Lake and its tributaries have had not only remarkably large runs of sockeye salmon during this period but also showed distinct population cycles (Eggers and Rogers 1987), and in recent years the runs have been very low. These changes in density, unrelated to degradation in habitat quality or access, have taken place during a period of dramatic shifts in climate (Mantua et al. 1997; Hilborn et al. 2003), making this an ideal system in which to study the interplay between these processes. We predicted that warmer conditions would be positively correlated with fry size at the end of the first summer, whereas intraspecific competition (within and between brood years) was predicted to correlate negatively with size.

Materials and methods

Study site and sampling

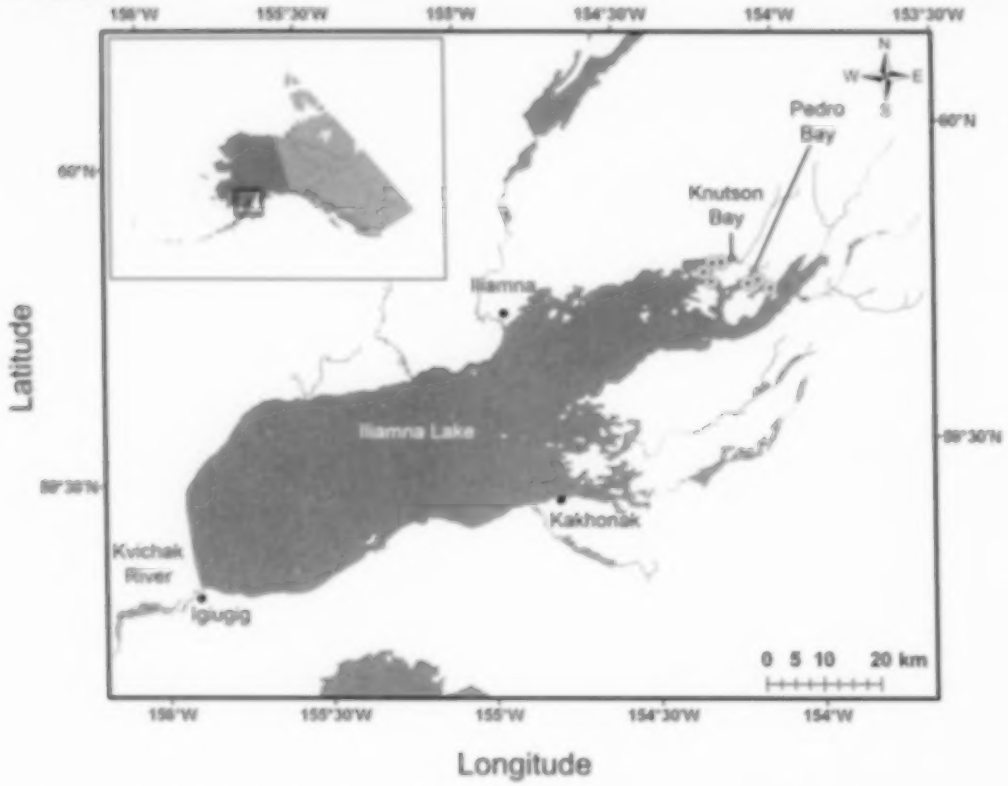
Iliamna Lake is the largest lake in Alaska, with a surface area of approximately 2622 km^2. It drains into the 90 km long Kvichak River, flowing into eastern Bristol Bay. The southwestern end of the lake is relatively wide, open, and shallow (average depth: 35 m), with few islands and a simple shoreline, whereas the northeastern end is narrow and deep (average depth: 80 m; max depth: ~300 m), with a complex shoreline and many islands (Fig. 1).

Juvenile sockeye salmon have been sampled annually in late summer by University of Washington staff since 1962. A 3 m × 3 m opening net was towed at the lake's surface behind and between two boats for 20 min at approximately 3 km·h^{-1}. Towing began approximately an hour after nightfall, to allow juvenile sockeye salmon to undergo their diel vertical migration, rising to surface areas to feed (Scheuerell and Schindler 2003), and to minimize visual gear avoidance. Some gear avoidance by larger individuals might occur; however, this would tend to homogenize the length distributions among years. The observed variation in lengths indicated underlying differences in size distributions among years. Catches were identified to species, individuals were measured for fork length, and a subsample was weighed. Sampling has taken place throughout the lake at standardized locations (Burgner 1964; Rich 2006), but spawning adults and juveniles are concentrated in the eastern end of the lake. In recent years, sampling has been most regular in two index sections (Knutson Bay and Pedro Bay, Fig. 1), and only the data from these sections were examined in this paper.

The two age classes of juvenile sockeye salmon, age-0 (fry) and age-1 (yearlings), were distinguished by inspection of size frequency distributions (Rich 2006). Within each year, the age classes were distinct; fry were typically <75 mm and yearlings were ≥75 mm; the long-term average lengths were 57 mm for fry and 91 mm for yearlings. We then calculated the average sockeye salmon fry length in a given year as the arithmetic mean length of fry caught in each section, weighted by their relative surface areas (Knutson Bay = 0.43, Pedro Bay = 0.57). Last, lengths of fry were standardized to length on 1 September because the actual sampling dates varied by a few days among years and sampling also took place on more than one night in most years. 1 September is near the end of the growing season for Bristol Bay sockeye salmon nursery lakes, and in most years the final sampling was conducted shortly before or after this date (Schindler et al. 2005). Lengths were adjusted by taking the product of the number of days between the sampling date and 1 September and the daily growth rate determined from that year, then adding or subtracting this to give an adjusted mean length. The annual growth rate was calculated from multiple sampling events that year. If sampling only took place at the end of the season, we used a value of 0.33 mm·day^{-1} (the long-term average growth rate for juvenile sockeye in this area of the lake; Rich 2006).

We initially used simple linear regressions to explore potential factors affecting fry growth and identify our predictor variables. Our first factor was fry density. There were no absolute estimates of fry abundance, so we used the Alaska Department of Fish and Game (ADF&G) counts of the adult sockeye salmon that entered the Iliamna Lake system to spawn as our index of juvenile fry density. These counts were offset by 1 year because the offspring from Brood

Fig. 1. Iliamna Lake, Alaska, USA, including index tow net sites (gray circles with centered black spot) used for long-term data collection in eastern end of the lake and three sites where environmental data were collected (black dots). Inset: Alaska and northwestern Canada, with study location highlighted.

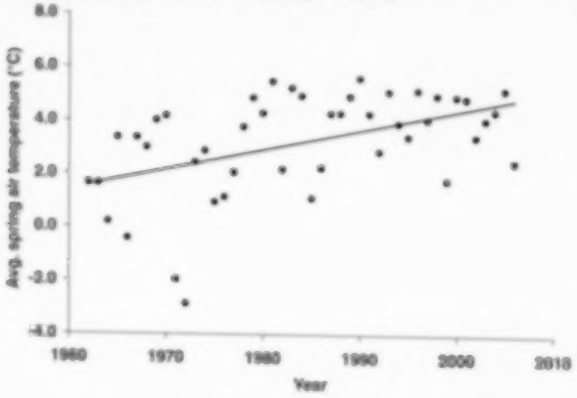


Year 1961, for example, were rearing in the lake as fry in 1962. The production of fry is likely to be related to the number of spawning adults in a nonlinear manner owing to density-dependent mortality (e.g., Essington et al. 2000). Therefore, we used the natural logarithm of parent escapement the year before as our metric of fry density.

Our second factor was the density of yearling sockeye salmon. We estimated their abundance as the natural logarithm of the number of age-2 smolts leaving Iliamna Lake in the following spring (as reported by ADF&G). The number of smolts includes fish rearing in Lake Clark, which would not compete with the fry in Iliamna Lake, resulting in an overestimate of competition. On the other hand, not all fish that were alive in the summer would have survived to the following spring, resulting in an underestimate of competition. Notwithstanding these offsetting sources of error, the smolt counts provided an index of competition between brood years. We did not use smolt counts for our estimate of fry density because the relationship between age-1 smolts and fry length explained far less variation than the parent escapement and fry length relationship. We felt justified in using smolt counts for the yearling density estimate because our yearling tow net index and smolt count relationship was strong ($r^2 = 0.78$, H. Rich, Fisheries Research Institute, unpublished data), and parent escapement lagged 2 years did not suitably account for life history transitions and sources of mortality that juveniles would experience over this time period.

The third factor hypothesized to affect growth was temperature, and we used the mean monthly air temperature from Intricate Bay, on the south side of Iliamna Lake, from March to June as an index of climate experienced by juvenile sockeye salmon each year. Spring air temperatures showed a significant warming trend in the Iliamna Lake area from 1962 to 2006. A simple linear model indicated that average spring air temperatures are about 3.3 °C warmer now than they were four decades ago (Fig. 2; $p < 0.001$, $r^2 = 0.25$). Spring air temperatures reflected other important environmental variables in this system, being positively correlated with spring water temperatures ($p < 0.0001$, $r^2 = 0.62$) and negatively correlated with day of ice break up ($p < 0.0001$, $r^2 = 0.45$). We tested several other combinations of months before our temperature index was selected for analysis of fry length, including winter (November–February, January–April, December–February), summer (June–August, July–September), entire sequences of first year life (November–October, September–October), and other variations of spring temperature (April–June, March–May, February–May, February–June). Intricate Bay (the Kakhonak village airfield: cdo.ncdc.noaa.gov/CDO/cdo) provided the region's most complete air temperature records over the period of this study (1962–2006), but in the 10 months

Fig. 2. Time series of spring air temperature (monthly average of March–June) from Intricate Bay, Iliamna Lake, Alaska, 1962–2006, showing warming trend ($r^2 = 0.25$, $p < 0.001$).



(scattered among years) when no records were collected at Intricate Bay, we used air temperatures collected at nearby Iliamna airport to complete the temperature record (Fig. 1). Linear regression revealed a strong correlation between the Intricate Bay and Iliamna airport records ($r^2 = 0.99$), and therefore we assumed that the temperatures used reflected local conditions. We used the air temperature data rather than water temperature or date of ice breakup because they were available for all months of the year rather than only the beginning of June, as was the case for the water temperature data.

In summary, our analysis used a 45-year time series of data including estimates of fry density and spring air temperatures on fry growth from 1962to 2006 (two-regressor model) and a shorter, 39-year time series (1962–2000) for which we had an additional estimate of yearling density (three-regressor model; see Table 1).

Time-series analysis

We used Gaussian state–space models (SSMs) to quantify the relative effects of three different factors on the growth of juvenile sockeye salmon in their first year of life: the density of their parents (and so, presumably, the abundance of fry), the density of older conspecifics from the previous year's cohort, and temperatures they experienced as newly emerged fry. The advantage of SSMs over conventional multiple regression is that in SSM the information on the sequence of observations is incorporated into the analysis, whereas in multiple regression the data from each year are treated as independent. SSM also address both observation and process errors. In ecological systems, the events in 1 year are often linked to those in previous and succeeding years by various processes, so SSMs may provide a better analytical tool, though the general findings are likely to be similar. SSMs are now being applied regularly for use with ecological data (e.g., Scheuerell and Williams 2005; Schindler et al. 2005; Ward et al. 2007).

The observed response variable at each time step t (Y_t) was modeled as a linear combination of a level parameter (θ_t), the product of a $1 \times m$ vector of regression parameters ($\boldsymbol{\beta}$) times an $m \times 1$ vector of predictor variables at time t ($\boldsymbol{X}_t$), and an error term (v_t) to form what is known as the observation equation:

$$(1) \qquad Y_t = \theta_t + \boldsymbol{\beta}\boldsymbol{X}_t + v_t \qquad v_t \sim N[0, V_t]$$

The normally distributed observation errors (v_t) have a mean 0 and time-dependent variance (V_t) that is estimated from all of the prior data.

A second equation known as the system equation allows the level parameter (θ_t) to change through time according to a first-order Markov process:

$$(2) \qquad \theta_t = \theta_{t-1} + \omega_t \qquad \omega_t \sim N[0, W_t]$$

where ω_t is the process error with mean 0 and variance W_t.

We began by fitting a so-called "reference" model containing only a level term, such that eq. 1 was simply

$$(3) \qquad Y_t = \theta_t + v_t \qquad v_t \sim N[0, V_t]$$

This random-walk model offered a means for comparing the relative performance of more complicated models containing explanatory variables. We fit all models using the "sspir" package in the R programming language (www.r-project.org).

We compared alternative models through the use of Akaike's information criterion corrected for small sample size (AIC_c), which balances model fit against overparameterization (Burnham and Anderson 2002). All models were ranked by increasing AIC_c, and the difference between each model and the best model was computed according to

$$(4) \qquad \Delta_i = AIC_{ci} - AIC_{cmin}$$

Burnham and Anderson (2002) suggested that when Δ_i equals 0–2, the level of empirical support for model i is "substantial"; 4–7 is "considerably less"; and >10 is "essentially none".

To compare the magnitude of the effect of each regressor on the dependent variable of each model, we calculated effect sizes as the product of the regression coefficient and the value of the independent variable in each year of the time series. Effect sizes were expressed in the units of the dependent variable, providing a simple indication of the magnitude of each explanatory variable on sockeye salmon fry size.

Results

For the 45-year time series (1962–2006), the model that included both spring air temperature and fry density best explained the variation in sockeye salmon fry length (Table 1). The model's fitted values matched the trends in the observed data in most instances (Fig. 3; $r^2 = 0.88$). The model including only spring air temperature performed better than the model including only sockeye salmon fry density, and both performed much better than the reference random-walk model (Table 1). The positive effect of air temperature was nearly three times larger than the negative effect of sockeye salmon fry density (mean effects: 7.90 mm for temperature and –2.64 mm for density; Fig. 3).

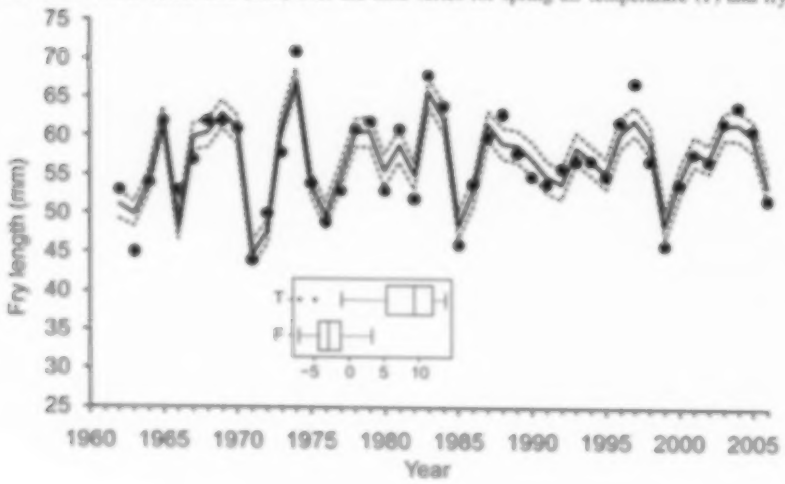
For the 39-year time series (1962–2000, for which we had data on yearling densities), the best model again had both fry density and spring air temperatures as predictors of fry

Table 1. Summary statistics from Gaussian state–space models (SSMs) to explain historical variation in juvenile sockeye salmon (*Oncorhynchus nerka*) length on 1 September from Iliamna Lake, Alaska.

Rank	Model	*n* (years)	*k*	NLL	AIC_c	Δ_i
Two regressors, 1962–2006						
1	Fry density + spring air	45	5	254.0	519.6	0.0
2	Spring air	45	4	302.9	614.8	95.2
3	Fry density	45	4	432.4	873.8	354.3
4	Reference	45	3	528.6	1063.8	544.2
Three regressors, 1962–2000						
1	Fry density + spring air	39	5	234.9	481.7	0.0
2	Fry density + yearling density + spring air	39	6	242.1	498.8	17.1
3	Spring air	39	4	278.2	565.5	83.8
4	Yearling density + spring air	39	5	286.2	584.3	102.6
5	Fry density + yearling density	39	5	368.0	747.9	266.2
6	Fry density	39	4	391.1	791.4	309.7
7	Yearling density	39	4	463.0	935.2	453.5
8	Reference	39	3	488.7	984.1	502.4

Note: Within each group, models are ranked in order of increasing predictive performance (i.e., lowest marginal negative log-likelihood (NLL)). The value of Akaike's information criterion corrected for small sample size (AIC_c) provides evidence in favor of a model compared with the best overall model. Values of Δ_i equal to 0–2 indicates the level of empirical support for model *i* is "substantial"; 4–7 is "considerably less"; and >10 is "essentially none" (Burnham and Anderson 2002). *k* represents the number of estimated parameters.

Fig. 3. Model prediction (±2 standard deviations, broken lines) and observed data for the fry density + spring air temperature model (1962–2006). Effect size plot inset shows mean effect size (mm) over the time series for spring air temperature (*T*) and fry density (*F*).

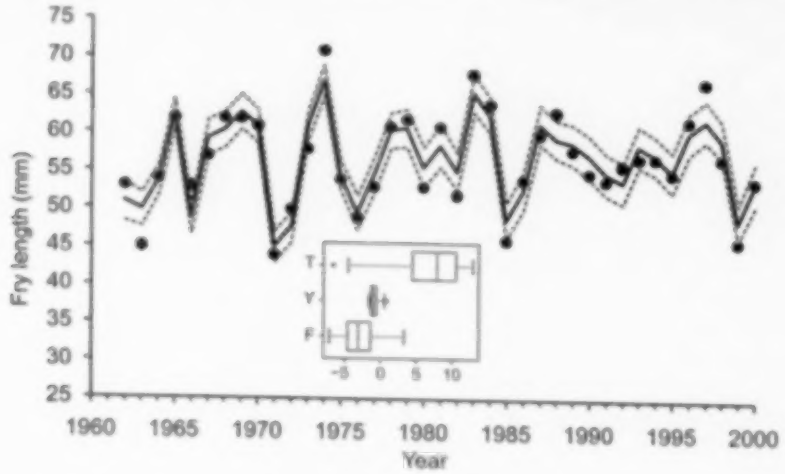


growth, followed by the model with spring air temperature and density estimates for both age classes of sockeye salmon (fry and yearling; Table 1). All models that included spring air temperature performed better than models containing only density estimates — sockeye fry alone, yearlings alone, or the combination of both juvenile age class densities (fry density and yearling density) — as predictor variables (Table 1). As with the longer time series, the model incorporating temperature and fry density captured the trends of the observed data (Fig. 4; $r^2 = 0.87$). The positive effect of temperature was the largest (mean = 7.09 mm), followed by the negative effect of fry density (mean = –2.86 mm), and finally the negative effect of yearling density (mean = –1.05 mm). The effect of temperature was thus greater than either fry or yearling density alone and about twice as large as the combined effect of both age classes of juveniles (Fig. 4).

Discussion

Spring air temperatures in the Iliamna Lake region of southwestern Alaska have warmed by about 3.3 °C since 1962, leading to significantly earlier date of ice breakup and warmer spring water temperatures at the lake's outlet (Rich 2006). The warming trend has had a strong positive effect on juvenile sockeye salmon growth in this system, combined with a weaker but also important effect of density. The temperature effect was the single most important pre-

Fig. 4. Model prediction (±2 standard deviations, broken lines) and observed data for the spring air temperature + fry density model (1962–2000). Effect size plot inset shows mean effect size (mm) over the time series for spring air temperature (*T*), yearling density (*Y*), and fry density (*F*).



dictor of fry growth, and all models including temperature performed better than models including estimates of density alone. The largest density-related effect resulted from competition within brood years, but there was also evidence that yearling density reduced growth of fry. The positive effect of spring air temperature was about three times as large as the negative effect of sockeye salmon fry density alone and about twice as large as the combined negative effects when both age classes of juvenile sockeye salmon were examined. These results were consistent with previous work in this system that used much shorter periods of record (Rogers and Poe 1984; Burgner 1987).

Warmer spring air temperatures can affect growing conditions in a number of ways. First, warmer temperatures can reduce duration of ice cover, lengthening the growing season. Schindler et al. (2005) showed that in nearby Lake Aleknagik, Alaska, spring ice breakup has become about 7 days earlier over a similar period (1962–2002). They attributed the earlier breakup to a long-term shift in baseline climatic conditions and also the warmer phase of the PDO that prevailed during this time period. Longer growing seasons should increase both primary and secondary productivity in the lake, increasing food supply and quality. Schindler et al. (2005) found that earlier ice breakup led to increased summer densities of zooplankton, the major food source for juvenile sockeye salmon. Interestingly, in Lake Aleknagik (with essentially the same sampling methods and period of record), the effects of fry density were more pronounced than climatic effects on fry growth (Schindler et al. 2005), and the number of yearling sockeye salmon in this lake is negligible, so the density effect is limited to a single age class. Iliamna Lake is larger, deeper (particularly in the eastern end where our index areas are located), and cooler than Lake Aleknagik (Burgner 1991; T. Quinn, Fisheries Research Institute, unpublished data), and so an increase in temperature has a proportionally greater effect by enhancing the physiological scope for growth. Moreover, although Iliamna Lake has many more returning adult sockeye salmon than Lake Aleknagik, the density is much lower because the former lake is so large (~18 adults·ha^{-1} since 1960 vs. 42 adults·ha^{-1} in Lake Aleknagik). Thus density-dependent processes seem to be much more important in Lake Aleknagik.

Warmer spring temperatures may also accelerate development of salmon embryos in the gravel, leading to earlier emergence of fry and enabling them to forage for a longer period of time before the onset of fall. Studies on the effects of reduced riparian zone vegetation (from experimental logging) revealed that milder temperatures led to earlier fry emergence in the spring, a longer growing season, faster growth in the summer, and a greater tendency to migrate to sea at age 1 rather than age 2 in British Columbia coho salmon (*Oncorhynchus kisutch*) (Holtby 1988; Holtby and Scrivener 1989). Atlantic salmon (*Salmo salar*) also grew faster in their first summer of life during warm years (Jonsson et al. 2005).

Early life stage influences affect later life performance such as growth, survival, and reproductive success in many taxa (Lindström 1999; Beckerman et al. 2003). Jonsson et al. (2005) found that climate (i.e., the North Atlantic Oscillation index) influenced water temperature and stream flow during the development of embryos, affecting the mean length of Atlantic salmon fry at the end of their first growing season and the proportion of the cohort that migrated to sea the following spring. In Iliamna Lake, summer temperatures (June–August) were less important than springtime temperatures (March–June) as an explanatory variable for sockeye salmon fry length, and this was also the case with Atlantic salmon (Jonsson et al. 2005).

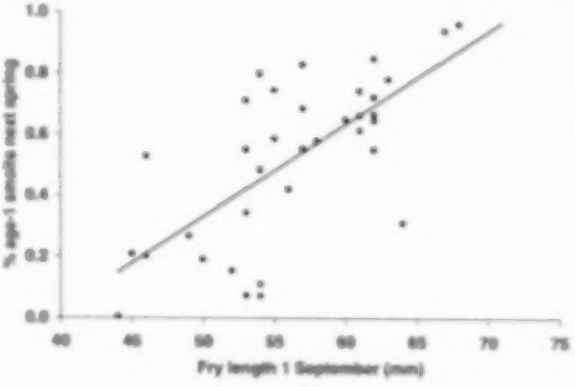
Sockeye salmon fry growth in Iliamna Lake was reduced by their cohort's density, as has been shown elsewhere (Burgner 1987; Kyle et al. 1988; Mazumder and Edmundson 2002), and this intrabrood competition was more than twice as strong as competition between cohorts (effect sizes: −2.86 vs. −1.05 mm). The fry greatly outnumber the yearlings (~10-fold; Rich 2006) in the eastern end of Iliamna Lake

where our index areas were located. Thus, despite the greater size of individual yearlings (7.5 vs. 1.7 g, based on mean weights pooled from catches between 15 August and 15 September), the competition from fry may exceed that of yearlings. However, densities of yearlings are higher in the western end of the lake (Burgner et al. 1969; Rich 2006) and so different results might have been found had that region been sampled over all the years. In other systems with multiple age classes of juveniles, the yearlings produced by large escapements reduced growth of the following year class (Selifonov 1970; Burgner 1987; Ruggerone and Rogers 2003). The Iliamna Lake system has been known for its cyclical population dynamics, with many instances of large (>6 million) escapements, sometimes occurring in two consecutive years, so both intra- and inter-brood effects are important in this system.

In the past decade, the Iliamna Lake system has seen the combined effects of warmer temperatures and reduced intraspecific competition. From 1960 to 1995, there were about 21 spawning adults·ha^{-1}, but from 1996 to 2005, the average has been only 8.5 adults·ha^{-1}, an almost 60% reduction in adult density. The system has not had consecutive large escapements since 1994–1995, and even the returns of 6.2 million in 1999 and 5.5 million in 2004 were small compared with the peak years in the past. This reduction in adult densities combined with warm conditions to increase fry size at the end of the first growing season. Fry size affects the proportion of a cohort that migrates to sea as 1 year olds (Burgner 1987; Rich 2006; Fig. 5, $r^2 = 0.48$), so the proportion of age-1 smolts leaving this system has increased. For smolt years 1993–2000, on average 72% of outmigrants were age-1, compared with the average of 48% age-1 smolts from the 1963–1992 smolt years. This may affect the population dynamics in the system by reducing interbrood competition for food in the lake, further reinforcing the tendency of fry to grow fast and leave the lake after a single year.

The fish may grow large enough to leave at age-1 the next spring but still be smaller than they would be as age-2 smolts. Data collected from this system (1962–2000 by ADF&G) indicated that age-1 smolts were 18% shorter and 43% lighter than age-2 smolts. Smolt size can have a positive effect on marine survival (Henderson and Cass 1991; Koenings et al. 1993). So, systems with historically high proportions of age-1 smolts may see beneficial effects of increases in temperature, whereas systems experiencing a shift to earlier age at migration may see lower survival (Quinn 2005). Smolt age and marine age are linked; age-2 smolts tend to spend 2 years at sea rather than 3 to a greater extent than age-1 smolts (Quinn 2005; Quinn et al. 2009). Of the adult sockeye salmon entering Iliamna Lake from 1979 to 2005, age-2 smolts produced 81.3% of those spending 1 year at sea, 52.6% of those spending 2 years at sea, and only 26.7% of those spending 3 years at sea (F. West, ADF&G, 333 Raspberry Road, Anchorage, AK 99518, USA, unpublished data). The age-1 smolts have reduced survival at sea because they are small when they enter the ocean and because they stay there longer and so have more exposure to predators and other mortality agents. Consistent with this scenario, Wood River system sockeye salmon have experienced improved productivity during the same period

Fig. 5. Iliamna Lake sockeye fry size at the end of the first growing season and the percentage of the cohort that leave Iliamna Lake as age-1 smolts the following spring, 1962–2000 ($r^2 = 0.48$, $p < 0.0001$).



when the Iliamna Lake system has experienced reduced productivity (Hilborn et al. 2003). The dynamics of fry growth in lakes Aleknagik and Iliamna reveal that ecological responses to climate change may not be regionally homogeneous and that the interplay between climate and other ecological factors such as competition may control how climate effects are expressed in population dynamics.

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Nutrient limitation of phytoplankton growth in Arctic lakes of the lower Mackenzie River Basin, northern Canada

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Abstract: Water chemistry and the nutrients limiting phytoplankton growth were examined in lakes located in the Northwest Territories, Canada, along a transect from the Mackenzie River Delta south to Travaillant Lake. This 230 km stretch spans gradients in vegetation types (tundra to boreal forest) and elevation (flooded by the Mackenzie River versus higher elevation lakes). Total phosphorus concentrations generally were typical of oligotrophic lakes (<10 $\mu g \cdot L^{-1}$), while nitrate and orthophosphate concentrations were below detection limits. Although some growth was noted in bioassays receiving single additions of nitrogen (N) or phosphorus (P), the greatest growth occurred in those bioassays in which nitrogen and phosphorus were added. This suggests that phytoplankton in the majority of study lakes were strongly co-limited by N and P irrespective of watershed type and Mackenzie River influence. Furthermore, it suggests that algal communities will be highly responsive to anthropogenic disturbances, which result in increased N and P loading to these lakes. Experimental results from March bioassays suggest that anthropogenic eutrophication would be exacerbated by increased temperatures (e.g., those associated with global warming).

Résumé : Nous avons étudié la chimie de l'eau et les nutriments qui limitent la croissance du phytoplancton dans des lacs des Territoires du Nord-Ouest, Canada, le long d'un transect allant du delta du Mackenzie vers le sud jusqu'au lac Travaillant. Cette section de 230 km traverse des gradients de types végétaux (toundra à forêt boréale) et d'altitudes (lacs inondés par le Mackenzie à lacs de plus haute altitude). Les concentrations de phosphore total (<10 $\mu g \cdot L^{-1}$) sont généralement celles de lacs oligotrophes typiques, alors que les concentrations de nitrates et d'orthophosphore se situent sous le seuil de détection. Bien qu'il se fasse de la croissance dans certains tests biologiques ayant reçu une seule addition d'azote (N) ou de phosphore (P), la croissance la plus forte s'observe dans les tests biologiques qui ont reçu une addition d'azote et de phosphore. Cela indique que le phytoplancton dans la majorité des lacs étudiés est limité conjointement par N et P, quels que soient le type de bassin versant et les effets du Mackenzie. De plus, les résultats laissent croire que les communautés d'algues pourraient réagir fortement à des perturbations anthropiques qui augmenteraient l'apport de N et de P dans ces lacs. Les résultats expérimentaux des tests biologiques de mars indiquent que l'eutrophisation anthropique serait exacerbée par des températures plus élevées (par ex., celles associées au réchauffement global).

[Traduit par la Rédaction]

Introduction

In many freshwater ecosystems, phosphorus (P) limits primary productivity and algal standing stocks (Schindler 1977; Edmondson 1991). This trophic status paradigm is based on data obtained from a wide variety of lakes from temperate North America and Europe (Schindler 1977). Experimental nutrient limitation studies have revealed a wide range of responses to P and nitrogen (N) additions, with greater growth often observed when P and N were added together than with single nutrient additions (Elser et al. 1990, 2007). Because of the paucity of limnological data from northern environments (Lim et al. 2001), high-latitude lakes were often not included in general models of algal nutrient deficiency (Brutemark et al. 2006; Keatley et al. 2007). Increasingly, evidence from the literature suggests that Arctic and subarctic lakes may not fit the paradigms proposed for temperate systems (Bonilla et al. 2005). Exposure of high-latitude lakes to persistent low sunlight, low temperatures, and extreme variations in day length may severely constrain plankton nutrient uptake, growth, and standing stocks (Keatley et al. 2007). Not surprisingly, phytoplankton response varies a great deal with nutrient enrichment bioassays showing P and (or) N limitation in the high Canadian Arctic (Bonilla et al. 2005 and references therein) and Alaskan foothill lakes (Levine and Whalen 2001). Pienitz et al.'s (1997*a*, 1997*b*) survey shows P limitation based on low concentrations of inorganic P in the low Arctic region. Debate therefore exists as to which nutrient (N, P, or both) typically limits phytoplankton in northern lakes (Flanagan et al. 2003).

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are of special interest with regard to nutrient limitation because global warming is relatively pronounced in these regions (Michelutti et al. 2003; Smith et al. 2005; Smol et al. 2005). Projected climate change effects, particularly in the western Arctic, will be greater than expected elsewhere (Rouse et al. 1997; Arctic Climate Impact Assessment 2005). Increased warming may have several consequences for lake productivity, including a longer growing season, warmer temperatures facilitating growth and nutrient regeneration, and increased nutrient inputs through permafrost melt and terrestrial inputs (Intergovernmental Panel on Climate Change 2001; Prowse et al. 2006). In addition, development in this region is expanding as the warmer climate makes the region more accessible and demand for natural resources intensifies with a growing world population (Mackenzie River Basin Board 2004). Consequently, understanding predisturbance baseline limnological conditions, especially with respect to nutrient response, is essential, as it will provide data on the natural variability of these lakes as well as reference for future monitoring programs (Pienitz et al. 1997*a*, 1997*b*).

While baseline studies were conducted as part of the proposed Mackenzie Gas Project environmental impact assessment, very limited information was obtained on dissolved and particulate nutrient levels in the lakes along the pipeline route (Imperial Oil Resources Ventures Limited 2004). As well, the other limnological studies that have been carried out in this region have focused on the Mackenzie River Delta (Fee et al. 1988; Squires and Lesack 2003) or further south in the basin (Pienitz et al. 1997*a*, 1997*b*). The overall goal of this study was to address knowledge gaps pertaining to lakes located along the proposed production facilities and pipeline route (Evans et al. 2007). As part of this work, sediment and water chemistry, benthos, zooplankton, and phytoplankton standing stocks and diversity are being characterized (Evans et al. 2007). This is the first of a series of papers originating from this research.

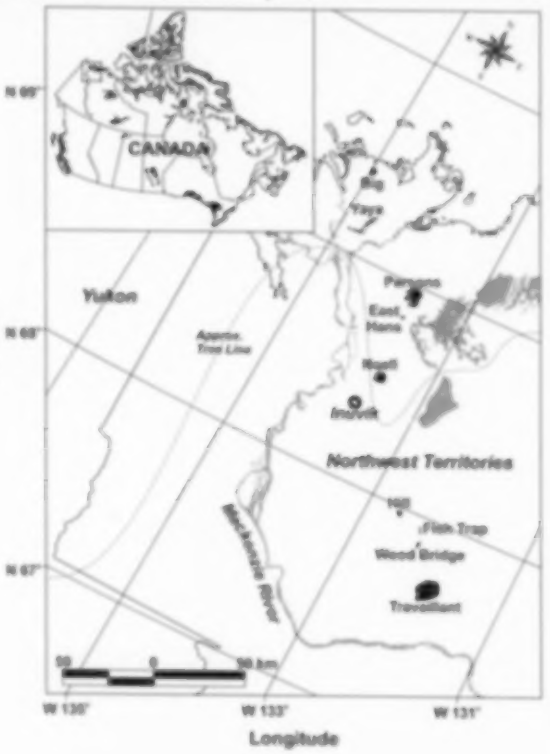
The main objectives of the present study were to (*i*) determine the main nutrient limiting phytoplankton biomass (measured as chlorophyll *a* (Chl *a*)) in a series of lakes located in the lower Mackenzie River Basin (MRB — specifically lakes along the pipeline route and running 130 km north in the tundra region from Inuvik to the outer Mackenzie River Delta and 100 km south into the boreal region); (*ii*) evaluate general nutrient sufficiency or deficiency of the algal community using protein to carbohydrate ratios; and (*iii*) assess the trophic status and spatial variability of particulate and dissolved nutrients in these lakes during summer and winter. Based on the studies of Pienitz et al. (1997*a*, 1997*b*) conducted in the general vicinity of our study area, we hypothesize that phytoplankton biomass will be P-limited. In addition, we hypothesize that phytoplankton will be nutrient sufficient during late winter because of nutrient regeneration and minimal uptake for growth.

Materials and methods

Study area and lake selection

The nine lakes chosen for this study are situated in the lower MRB, northern Canada, and lie along a latitudinal gradient between 67°43′N and 69°23′N (Fig. 1, Table 1).

Fig. 1. Map of Canada (inset) showing the lower Mackenzie River Basin, Inuvik, and location of study lakes.



They are a subset of a larger series of lakes sampled as part of baseline characterization of lakes along the proposed pipeline route. Climate here is highly variable because of large geographic diversity and proximity to the Beaufort Sea. Nevertheless, Inuvik has a transitional climate between Arctic and subarctic, with long, cold winters and short, cool, dry summers, with ice-free conditions lasting from mid-June to mid-September. For the period 1971–2000, mean air temperature was –8.8 °C, while mean annual total precipitation was 248.4 mm, 131.4 mm of which fell as snow. Summer in the high Arctic brings uninterrupted sunlight for almost 6 months, with temperatures briefly reaching into the 20 °C range in July. Winter is dark, with temperatures falling to –50 °C and lower (Environment Canada 2005, Climate Normals 1971–2000).

The Tundra Ecological Zone north of Inuvik is a dry, cold, treeless desert characterized by dwarf shrubs, mosses, and sedges that have adapted to the short growing season. South of this region is the Forest Ecological Zone. The northern boundary here represents the tree line, and tree size and forest density increase from north to south. Low precipitation and bitterly cold winters stunt tree growth in the northern part of this zone. Small, scattered clumps of dwarf white spruce (*Picea glauca*), tamarack (*Larix laricina*), and dwarf birch (*Betula nana*) occur on warmer, sheltered sites, while shrub communities are found in lower, poorly drained slopes with white spruce and willow (*Salix* spp.) found along riparian areas (Imperial Oil Resources

Table 1. Geographic and morphological features of study lakes.

Parameter	Travaillant Lake	Wood Bridge Lake	Fish Trap Lake	Hill Lake	Noell Lake	East Hans Lake	Parsons Lake	Yaya Lake	Big Lake
Location									
Latitude (N)	67°43′	67°52′	67°56′	67°58′	68°21′	68°50′	68°58′	69°11′	69°23′
Longitude (W)	131°41′	132°09′	132°13′	132°32′	133°43′	133°39′	133°39′	134°37′	134°32′
Surface area (ha)	11 360	494	338	810	302	360	6320	1950	1180
Mean depth (m)	4.7	8.7	13.9	1.8	5.6	1.5	3.7	28.0	3.0
Elevation (m)	131.1	243.8	243.8	225.3	91.0	30.5	30.5	5.0	2.2

Ventures Limited 2004). This area is also characterized by impressive glacial landforms such as giant eskers, kettle lakes, and patterned ground formations created by intense frost action in the soil.

The study transect began at Big Lake (site of one of the three proposed drill pads), moved south to Parsons Lake (site of the third drill pad), and ended at Travaillant Lake. Thus, lakes south of Inuvik (Hill, Fish Trap, Wood Bridge, and Travaillant lakes) are below the tree line, while those north (Big, Yaya, Parsons, East Hans, and Noell lakes) are located in the Arctic tundra ecozone. Many delta lakes, including Big and Yaya, are flooded annually because of their low elevation and close proximity to the Mackenzie River. Elevation rises to 244 m in the southern end of the study transect, with water input as rainfall, snowmelt, and permafrost melt. Most lakes are shallow with depths less than 10 m, although Fish Trap Lake reaches at least 14 m in depth and Yaya over 30 m.

Study lakes

In August 2006, Big and Parsons lakes were selected for nutrient limitation studies because of their close proximity to proposed drill pads and also because they represented flooded and nonflooded lakes, respectively. In March 2007, we were unable to visit these study lakes because of licensing difficulties and consequently focused our sampling on Fish Trap, Hill, Travaillant, and Wood Bridge lakes, which are located below the tree line. In early July 2007, another Environment Canada field party working in the area north of Inuvik provided us with water for experimental studies from Parsons, East Hans, and Noell lakes. In late July 2007, we conducted another limnological survey and selected Big, Yaya, Parsons, and Travaillant lakes for further experimental study. Yaya Lake was selected because of its depth. Big and Parsons lakes to investigate interannual variability in study findings, and Travaillant Lake to compare winter and summer conditions in the same lake.

Water chemistry

Lakes were accessible only by aircraft and so were sampled using a DHC-2 Beaver aircraft equipped with floats (summer sampling) or a helicopter (March study). A YSI 6600 multiparameter sonde (Hach Environmental) was used to measure temperature, conductivity, pH, and dissolved oxygen with depth. Water samples were collected ~30 cm below the lake surface using triple-rinsed, acid-washed Nalgene bottles and at 1 m from the bottom using a Niskin bottle; water chemistry means for the two depths are reported, except where stratified. Nalgene bottles were placed on freezer packs in coolers until return to the laboratory later in the day. At the end of the day, water was filtered through 153 μm Nitex mesh to remove detritus and larger zooplankton and then subsampled for particulate nitrogen (PN), total dissolved nitrogen (TDN), ammonia (NH_3), nitrate–nitrite (NO_2 + NO_3), total phosphorus (TP), dissolved phosphorus (DP), orthophosphate (ortho-P), particulate carbon (PC), dissolved organic carbon (DOC), and Chl *a*. Particulate phosphorus (PP) was estimated as the difference between TP and DP. Total nitrogen (TN) was calculated as the sum of TDN and PN. All analyses were conducted following the methods described in Environment Canada (1992).

Phytoplankton biomass was measured as Chl *a* according to the method of Nusch (1980). Water (500 mL to 1 L) was filtered through 47 mm GF/C filters (nominal pore size 1.2 μm) and then immersed in 10 mL of 90% ethanol in a 50 mL Falcon centrifuge tube and frozen. Samples were stored in the freezer until extraction. Chl *a* was then determined using a Turner Designs fluorometer (Sunnyvale, California, USA) equipped with narrow bandpass filters that screen out possible interference from pheopigments. Accordingly, Chl *a* values were not corrected for pheopigments.

P and N deficiencies as assessed by N, P, and C ratios

Algal nutrient deficiencies were assessed by using ratios developed by Redfield (1958) and Smith (1982). The Redfield method uses sestonic ratios of PC, PN, and PP on a molar basis; PC:PP ratios > 106 and PN:PP > 16 infer P deficiency, while PC:PN ratios > 6.6 are indicative of N deficiency. The Smith method is based on weights (or concentrations, $\mu g \cdot L^{-1}$) of TN and TP in ambient water. Ratios ≥ 17 infer that TP drives chlorophyll biomass, while TN drives biomass at ratios ≤ 10. N and P co-limitation of algal growth occurs when TN:TP ratios are between 10 and 17.

General nutrient deficiency as assessed by protein to carbohydrate ratios

Protein to carbohydrate ratios have been used as general indicators of nutrient deficiency for both laboratory and field populations of phytoplankton (Healey and Hendzel 1980). Ratios > 1.2 indicate no nutrient deficiency, while those < 0.7 indicate extreme deficiency (Pick 1987). This ratio does not distinguish between N or P deficiency.

For carbohydrate and protein analyses, three replicate 500 mL water samples were filtered onto combusted GF/C filters. Details of the carbohydrate protocol are described in Pick (1987) and the protein protocol in Waiser and Robarts (1995). Briefly, particulate protein was measured by the Folin–Lowry method using a Sigma kit (Rausch 1981; Sigma Chemicals, St. Louis, Missouri). Because this method was found to inadequately extract protein on its

Table 2. Water chemistry of study lakes (n = 9).

Parameter	Travaillant Lake (Summer)	Wood Bridge Lake (Summer)	Fish Trap Lake (Summer)	Hill Lake (Summer)	Noell Lake (Summer)	East Hans Lake (Summer)
Temperature (°C)	16.9±0.3	16.3±1.0	16.8±0.0	16.1±0.0	15.6±0.6	13.7±1.2
pH	8.2±0.1	7.8±0.2	7.6±0.3	8.3±0.0	8.2±0.1	8.1±0.1
Conductivity (μS·cm^{-1})	118.5±0.3	83.0±0.0	82.5±2.5	75.0±0.0	67.5±0.3	84.0±1.2
DO (mg·L^{-1})	9.5±0.1	8.4±0.8	9.3±0.0	10.4±0.0	9.8±0.1	10.9±0.1
Turbidity (NTU)	0.6±0.0	0.6±0.1	2.4±1.8	5.4±0.4	0.5±0.2	6.1±0.7
TP (μg·L^{-1})	2.3±0.1	5.5±0.5	12.5±3.5	38.5±0.5	7.8±3.1	36.3±9.8
TN (μg·L^{-1})	436.0±44.3	654.5±8.5	721.5±38.6	1358.5±44.6	201.5±10.6	779.8±29.4
DP (μg·L^{-1})	1.8±0.4	1.0±0.0	3.0±1.0	5.0±0.0	1.8±0.4	6.3±2.2
Ortho-P (μg·L^{-1})	1.8±0.4	1.0±0.0	1.0±0.0	1.0±0.0	1.8±0.4	1.8±0.4
TDN (μg·L^{-1})	318.0±7.6	456.5±4.5	522.5±37.6	500.5±9.5	192.8±7.4	441.0±9.5
NH_3 (μg·L^{-1})	11.3±1.7	14.5±0.5	41.5±26.6	14.0±0.0	6.3±1.4	15.3±0.9
NO_2 + NO_3 (μg·L^{-1})	5.0±0.0	5.0±0.0	19.5±14.5	5.0±0.0	5.0±0.0	5.0±0.0
DOC (mg·L^{-1})	10.6±0.8	14.0±0.2	13.7±0.2	11.1±0.1	4.9±0.5	11.8±0.6
PP (μg·L^{-1})	0.5±0.3	4.5±0.5	9.5±2.5	33.5±0.5	6.0±3.5	30.0±7.7
PN (μg·L^{-1})	118.0±47.1	198.0±13.0	199.0±1.0	858.0±35.1	8.8±3.8	338.8±21.1
PC (μg·L^{-1})	149.5±20.5	244.0±67.2	333.0±29.1	3905.0±125.4	103.0±16.5	2035.0±133.8
Chl a (μg·L^{-1})	1.7±0.1	3.1±1.6	3.3±2.5	26.3±5.9	1.6±0.1	23.8±2.9

Note: Lakes are arranged in order of increasing latitude. DO, dissolved oxygen; NTU, nephelometric turbidity units; TP, total phosphorus; TN, total ticulate nitrogen; PC, particulate carbon; Chl a, chlorophyll a; ND, not determined.

own, an initial protein extraction step was added. This entailed adding 0.5 mL of Milli-Q water and 0.5 mL of 1 mol·L^{-1} sodium hydroxide (NaOH) to the filter and incubating in an 80 °C water bath for 10 min. Following this step, the Lowry reagents were added (cf. Rausch 1981). Bovine serum albumin was used for the calibration curve, and protein was expressed as milligrams of protein (bovine serum albumin equivalent) per litre. Particulate carbohydrate was measured using the phenol–sulfuric acid method. Reagent-grade glucose was used for the calibration curve, and carbohydrate was expressed as milligrams of glucose equivalent per litre (Pick 1987).

Nutrient bioassays

Four nutrient-enrichment bioassay experiments — one in winter (March 2007) and three in summer (August 2006, early and late July 2007) — were performed using water from nine different lakes. Bioassays using natural assemblages of phytoplankton followed the US Environmental Protection Agency protocol for algal assay bottle tests (Elser et al. 1990; American Public Health Association 1999). Treatments were control (no nutrient addition), +N, +P, and +N+P and were run in triplicate. This factorial design was used to separate effects of combined nutrient additions (+N+P) from individually added nutrients (+N or +P) (Elser et al. 1990; Waiser and Robarts 1995). Nutrient treatments were 32 μmol·L^{-1} N (i.e., 448 μg·L^{-1}) as ammonium nitrate (NH_4NO_3) and 2 μmol·L^{-1} P (i.e., 62 μg·L^{-1}) as potassium phosphate (KH_2PO_4) in the single nutrient addition treatments and a combination of both in the +N+P treatment. In the +N+P treatment, the molar ratio of addition was 16:1. These concentrations ensured that nutrients were not depleted during the experiments.

For all bioassays, water samples were prefiltered through 153 μm Nitex mesh (as described above); 100 mL was subsequently apportioned into each acid-washed, 250 mL autoclaved glass flask. Nutrients were added as above. Following treatment, flasks were well mixed, stoppered with autoclaved foam plugs, and gently shaken on a shaker table. Bioassays were incubated at 18 °C under a 16 h light:8 h dark cycle in a temperature-controlled room. Light levels (20 μmol·s^{-1}·m^{-2}) were measured with a quantum light sensor (LI-COR, model 190).

There was a slight modification to the above protocol in the March 2007 experiment. This study was done at a lower temperature and light level (6 °C and 10 μmol·s^{-1}·m^{-2}, respectively) to closely replicate in situ light and temperature. Irradiance was adjusted with layers of neutral density screen. After 17 days of incubation with no increase in absorbance, both temperature and light were gradually increased to 10 °C and 20 μmol·s^{-1}·m^{-2}, respectively, and the experiment was run for an additional 10 days.

Phytoplankton response to nutrient additions was followed by measuring absorbance over time. On each day (or predetermined sampling period), a 2.5 mL sample was withdrawn from each flask, pipetted into a quartz cuvette (1 cm pathlength), and absorbance readings taken at 665 nm. The spectrophotometer was zeroed with 0.45 μm cellulose-acetate-filtered lake water. All experiments were concluded when absorbance values did not change (or actually decreased) over two consecutive sampling periods, usually after 18–20 days. For each treatment, a plot of absorbance versus time was constructed. At the beginning and end of the experiment, water for Chl a was filtered and analyzed as above.

Statistical analysis

Data on the water chemistry are reported as means (n = 3; ±1 standard error) for summer (July and August) and winter (March) for each study site and the two depths sampled for most lakes and times. Only one depth was sampled in Hill Lake in March. Where concentrations were below de-

Parsons Lake (Summer)	Yaya Lake (Summer)	Big Lake (Summer)	Travaillant Lake (March)	Wood Bridge Lake (March)	Fish Trap Lake (March)	Hill Lake (March)
14.9±0.7	14.1±0.5	14.1±0.7	1.1±0.9	1.9±1.6	1.4±1.1	0.4
8.0±0.2	8.4±0.0	8.5±0.0	8.1±0.0	7.7±0.1	7.6±0.3	7.5
67.0±0.6	291.0±2.2	251.3±10.3	149.0±3.0	101.0±0.0	111.0±13.0	170.0
10.0±0.3	10.5±0.1	10.5±0.3	15.4±0.3	10.8±2.6	8.9±4.2	0.4
2.4±0.1	0.5±0.0	2.6±0.8	ND	ND	ND	ND
16.0±8.1	3.75±0.0	6.5±2.3	5.5±0.5	8.0±0.0	9.0±0.0	38.0
584.0±40.4	277.5±18.73	266.3±9.8	517.0±41.1	674.0±15.0	815.0±59.2	8520.0
3.8±0.7	1.75±0.5	2.3±0.1	2.5±0.5	5.5±0.5	6.5±0.5	7.0
1.8±0.4	1.75±0.5	1.8±0.4	1.0±0.0	1.0±0.0	1.0±0.0	1.0
372.0±5.2	196.5±9.5	207.8±9.2	419.0±9.0	566.0±11.0	661.0±58.2	1300.0
11.5±2.5	9.0±3.5	8.8±1.6	8.5±0.5	9.5±0.5	10.0±0.0	402.0
5.0±0.0	5.0±0.0	5.0±0.0	27.0±3.0	50.0±6.0	96.0±42.1	5.0
5.8±0.7	3.95±0.7	6.6±1.1	10.8±0.2	15.3±0.4	16.1±0.1	20.4
12.3±7.4	0.5±0.5	4.3±2.5	3.0±0.0	2.5±0.5	2.5±0.5	31.0
212.0±42.3	81.0±28.2	58.5±13.3	98.0±32.1	108.0±4.0	154.0±1.0	7220.0
1215.0±117.0	138.5±11.67	304.0±25.3	5.0±0.0	5.0±0.0	5.0±0.0	686.0
11.8±1.7	1.8±0.1	3.0±0.2	1.2±0.9	0.3±0.3	0.5±0.4	9.1

nitrogen; DP, dissolved phosphorus; TDN, total dissolved nitrogen; DOC, dissolved organic carbon; PP, particulate phosphorus; PN, par-

tection limits, half the detection limit was used in calculating the lake seasonal mean.

For bioassay experiments, Chl *a* data was logarithmically transformed ($\log_{10}$) to meet normality requirements of parametric statistical analysis. In all experiments, a one-way analysis of variance (ANOVA) on Chl *a* concentrations followed by Tukey's honestly significant difference post hoc test was used to test for differences between treatments. For absorbance measurements, a repeated-measures (RM) ANOVA test was used to test for differences between treatments relative to controls. The significance level for testing was $P < 0.05$. All statistical analyses were performed using STATISTICA (Statsoft, Inc., Tulsa, Oklahoma).

Results

Limnological features of study lakes: summer

Average summer water temperature decreased with increasing latitude from 16.9 °C at Travaillant Lake to 14.1 °C at Big Lake; average water temperatures are based on the entire water column, except for Yaya and Fish Trap lakes where epilimnetic temperatures are used because of a well-developed hypolimnion (Table 2, Imperial Oil Resources Ventures Limited 2004). Specific conductivity was highest in Big and Yaya lakes, which receive water from the Mackenzie River, and substantially lower elsewhere. Dissolved oxygen concentrations were high, ranging from 8.4 to 10.9 mg·L^{-1}. Turbidity was low in all lakes with no obvious spatial gradient. DOC concentrations were highest in lakes south of Inuvik but also in East Hans Lake (a small lake). TP concentrations (<10 µg·L^{-1}) generally were characteristic of oligotrophic lakes, with higher concentrations observed in Parsons, East Hans, Hill, and Fish Trap lakes. TN followed a similar spatial pattern. DP, ortho-P, $NO_2 + NO_3$, and NH_3 concentrations were exceedingly low and often below detection limits. Chl *a* concentrations were low (<5 µg·L^{-1}), with higher concentrations observed in Parsons, East Hans, and Hill lakes.

Limnological features of study lakes: winter

Ice thickness during the March 2007 sampling ranged from 0.8 to 0.9 m and was overlain by 0.5–0.6 m of snow (Table 2). Water temperature was low (0.4–1.9 °C) and was well oxygenated (dissolved oxygen levels from 8.9 to 15.4 mg·L^{-1}), except for Hill Lake, which was anoxic. Specific conductivity was substantially higher than in summer, reflecting freeze-out of salts during ice formation. TP, TN, and Chl *a* concentrations remained low in all lakes except Hill. In Hill Lake, there were high concentrations of TP, TN, TDN, NH_3, PC, PN, and Chl *a*, as well as low concentrations of DP and ortho-P.

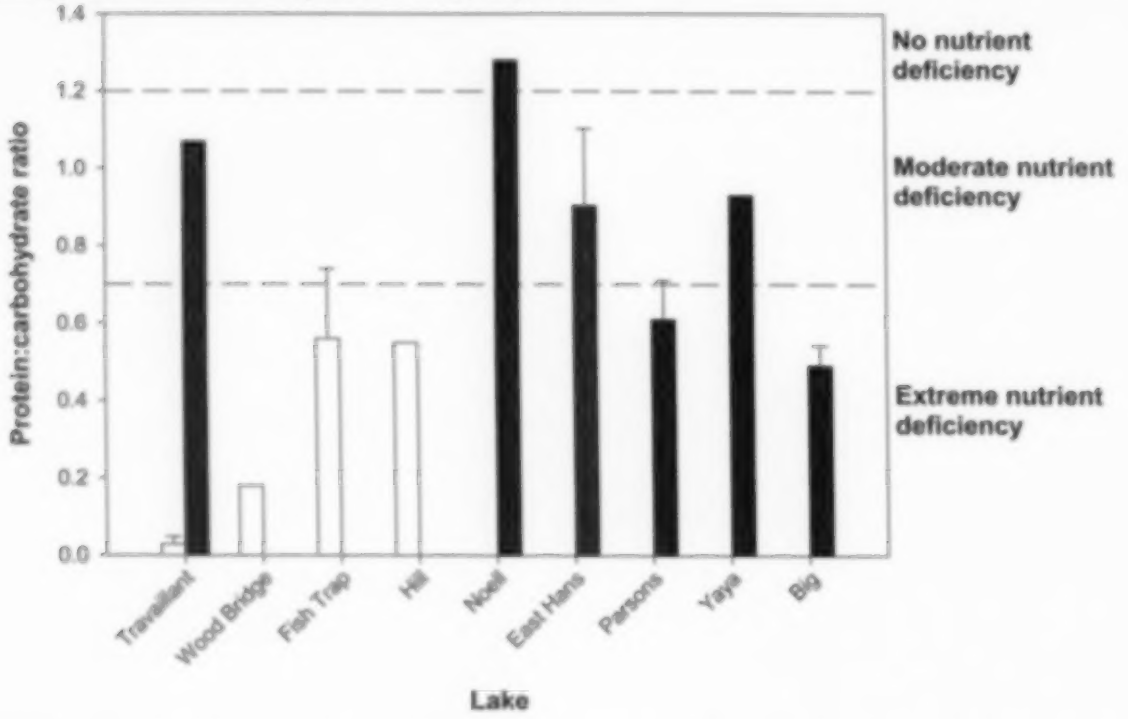
Nutrient deficiency: summer

Protein to carbohydrate ratios indicated no nutrient deficiency for Noell Lake and moderate deficiency for Travaillant, East Hans, and Yaya lakes. Extreme deficiencies were noted in Parsons and Big lakes (Fig. 2). Nutrient deficiency, as assessed by the total nutrient ratios (TN:TP, Fig. 3), indicated that all lakes were strongly P deficient. Based on PC:PN ratios (Fig. 4*a*), N limitation was evident in nearly all lakes located north of Inuvik, while PC:PP ratios (Fig. 4*b*) indicated P limitation in both Travaillant and East Hans and possibly Parsons lakes. PN:PP ratios (Fig. 4*c*) suggested P limitation in most lakes, except Noell Lake.

Nutrient deficiency: winter

According to protein to carbohydrate ratios, all lakes sampled during this period showed extreme nutrient deficiency (Fig. 2). When total nutrient ratios were examined (Fig. 3), all lakes showed P limitation, similar to results obtained for summer samples. In addition, sestonic PC:PN showed N limitation in Hill Lake (Fig. 4*a*), PC:PP did not

Fig. 2. Sestonic protein to carbohydrate ratios measured from surface waters of study lakes. Solid bars indicate summer; open bars show winter. Data are means of three replicates (±1 standard error, SE). The horizontal reference lines indicate severity of nutrient deficiency as defined by Pick (1987). Lakes are arranged in order of increasing latitude.



indicate P limitation in any study lake (Fig. 4*b*), and PN:PP showed P limitation in all sites (Fig. 4*c*).

Bioassay results: summer

Bioassays were performed on water from Big Lake, the outermost lake in the Mackenzie River Delta, in August 2006 (supplemental Fig. S1[2]) and late July 2007 (Fig. 5*a*). (Because bioassay results showed similar trends, only results of winter (March 2007) and late July 2007 are included herein. All other plots are presented as supplementary material in Figs. S1 and S2.[2]) Similar results were obtained on both occasions with the most pronounced growth in the +N+P additions and substantially less growth in the N only or P only treatments.

Bioassay experiments were conducted for Parson Lake in August 2006, early July 2007 (supplemental Fig. S1[2]), and late July 2007 (Fig. 5*b*). In the August and early July experiments, a statistically significant increase in growth was only observed in the +N+P treatment. Chl *a* concentrations (Fig. 5*e*) were higher in +N+P in August 2006 and early July 2007, with the P addition also having higher concentrations than the control in early July. Similar results were obtained in the late July 2007 experiment, although the +N addition also was stimulatory. With respect to the absorbance measurements, only the +N+P treatment was significantly different from the control.

According to the absorbance results, algal growth in Travaillant Lake (Fig. 5*c*) was co-limited by N and P, with Chl *a* concentrations (Fig. 5*e*) significantly higher in the +N+P addition compared with the control ($P < 0.05$).

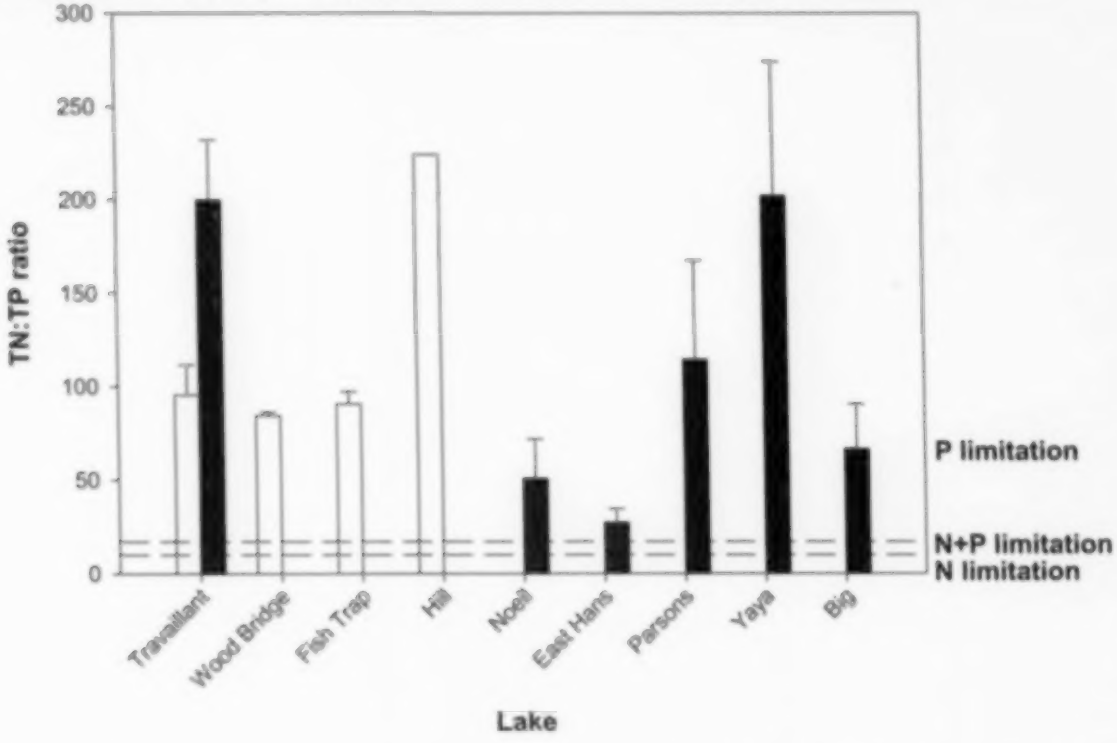
Yaya Lake (late July 2007, Fig. 5*d*) bioassays showed modest algal growth with +N or +P additions but statistically greater growth with +N+P, again suggesting co-limitation. Although higher Chl *a* concentrations were statistically significant in the +P treatments, relative to the control, growth with +P was substantially less than with +N+P.

Bioassay results: winter

Phytoplankton were slow to respond to nutrient additions in the March bioassay, with growth only detected when water temperatures were raised from 6 to 10 °C and light from 10 to 20 μohm-s^{-1}-cm^{-2} (Figs. 6*a*, 6*b*, 6*c*, and 6*d*). Based on absorbance changes, the strongest growth occurred in the +N+P additions, with the exception of Travaillant Lake where P addition was equally stimulatory. At the end of the experiment, Chl *a* concentrations in the +N+P treatments for all four lakes were significant relative to their respective control and in P additions for Fish Trap, Hill, and Wood Bridge lakes (Fig. 6*e*).

[2] Supplementary data for this article are available on the journal Web site (cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3884. For more information on obtaining material refer to cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

Fig. 3. Nutrient (total nitrogen to total phosphorus (TN:TP)) ratios calculated from epilimnetic waters of study lakes. Solid bars indicate summer; open bars show winter. Data are means of three replicates (+1 standard error, SE). The horizontal reference lines depict nutrient ratios and boundaries for sufficiency or deficiency. Lakes are arranged in order of increasing latitude.



Bioassay results: synthesis

Overall, the RM ANOVA test on absorbance through time indicated that phytoplankton communities were co-limited by N and P in nearly all lakes, with absorbance in the N+P treatment significantly greater ($P < 0.05$) than controls or single nutrient additions in 12 of 13 bioassays (92%) conducted. The only instance where there was no significant effect of +N+P was in the March bioassay for Travaillant Lake (Fig. 6c). In cases where a single nutrient (N or P) enhanced algal biomass, the effect of P was greater than that of N.

Similarly, the one-way ANOVA tests on Chl *a* concentrations showed that all bioassays responded positively to +N+P treatments relative to controls or individual additions of N or P. When individual additions of N or P proved stimulatory, the effect of P was relatively greater than that of N.

Discussion

Phytoplankton response to nutrient additions

Although bioassays have been criticized on grounds that containment may cause artifacts (cf. Elser and Kimmel 1986; Hecky and Kilham 1988), they are commonly used and appear to be reasonable indicators of algal nutrient limitation (Healey and Hendzel 1980; Davies et al. 2004; Groeger 2007). Nutrient enrichment bioassays in this study clearly showed that phytoplankton communities in lakes to the east of the Mackenzie River were simultaneously limited by N and P. This type of limitation implies that both N and P are in short supply relative to phytoplankton needs, and contemporaneous additions of both nutrients are therefore required to stimulate substantial growth (Dodds et al. 1989). In most of our study lakes, TP concentrations were low (<10 $\mu g \cdot L^{-1}$), confirming that these lakes are phosphorus-poor oligotrophic systems. In addition, concentrations of other dissolved inorganic nutrients such as $NO_2 + NO_3$, NH_3, DP, and ortho-P were exceedingly low or undetectable in the surface waters at most sites. These nutrients are preferentially taken up for growth and rapidly depleted by phytoplankton communities during summer stratification in many temperate lakes (Davies et al. 2004), and their ambient concentrations are therefore a reliable measure of phytoplankton nutritional status (Hecky and Kilham 1988). Similar low levels of inorganic nutrients have been observed in Mackenzie River Delta lakes (Squires and Lesack 2002), lakes on the Tuktoyaktuk Peninsula (Anema et al. 1990; Ramlal et al. 1991), lakes situated between Yellowknife and Contwoyto, Northwest Territories (Pienitz et al. 1997*a*, 1997*b*), and other high-latitude lakes (Levine and Whalen 2001).

Remarkably, N and P co-limitation was observed in all study lakes irrespective of watershed characteristics (tundra versus boreal), flooding regime (flooded versus nonflooded),

Fig. 4. Redfield seston ic ratios (particulate carbon to particulate nitrogen (PC:PN), particulate carbon to particulate phosphorus (PC:PP), and particulate nitrogen to particulate phosphorus (PN:PP)) derived from epilimnetic waters of study lakes. Solid bars indicate summer; open bars show winter. The mean molar ratios on *Y* axes are plotted in log scale to show very low values; horizontal reference lines represent nutrient (molar) ratios and boundaries for sufficiency or deficiency as outlined by Redfield (1958). Lakes are arranged in order of increasing latitude.

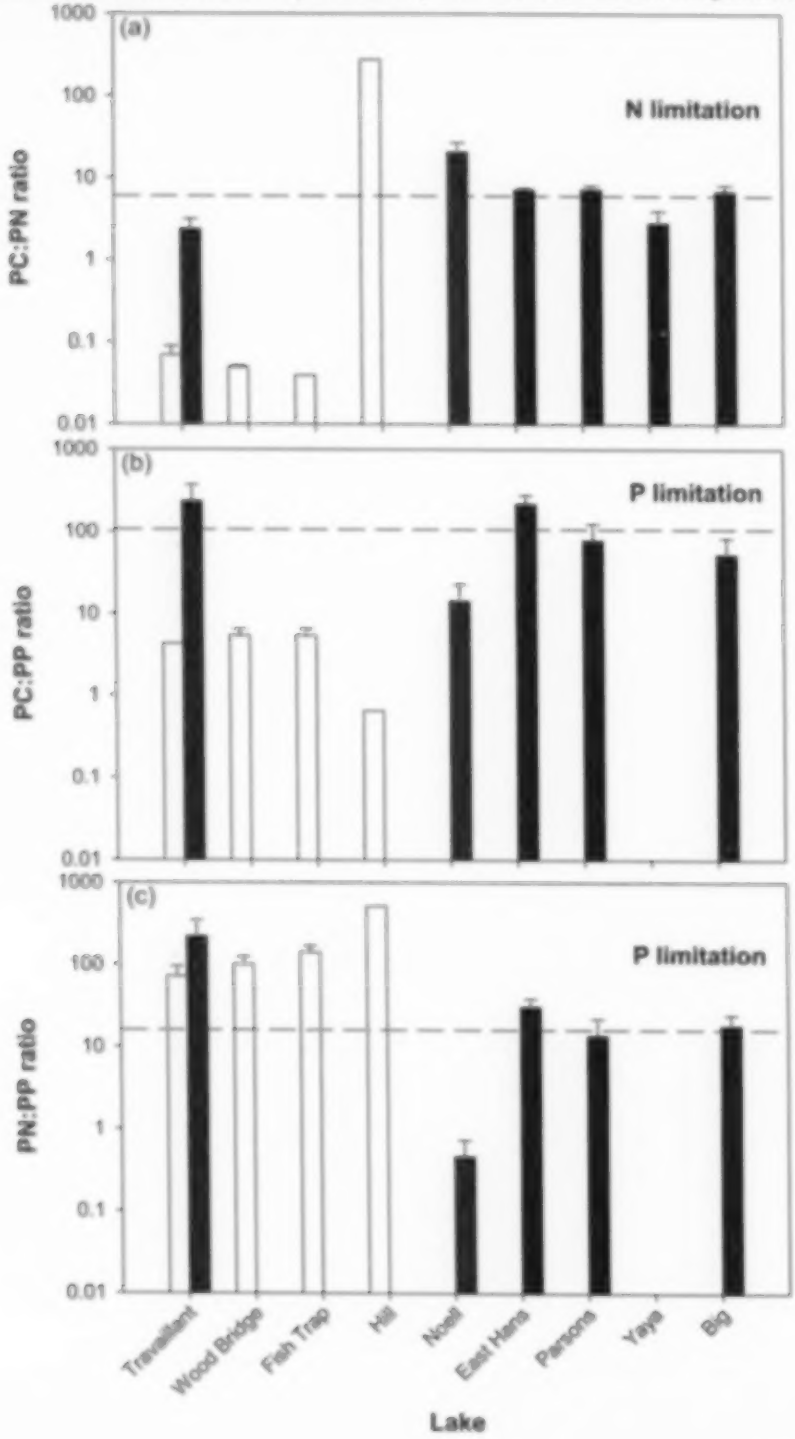


Fig. 5. Absorbance readings for summer (late July 2007) nutrient enrichment bioassays: (*a*) Big Lake, (*b*) Parsons Lake, (*c*) Travaillant Lake, (*d*) Yaya Lake, and (*e*) Chl *a* concentrations from bioassays. Data represent the mean of triplicate flasks (±1 standard error, SE). Significant treatment effects ($P < 0.05$) relative to control are marked with asterisks. Control, ●; +N, ○; +P, ▼; +N+P, △.

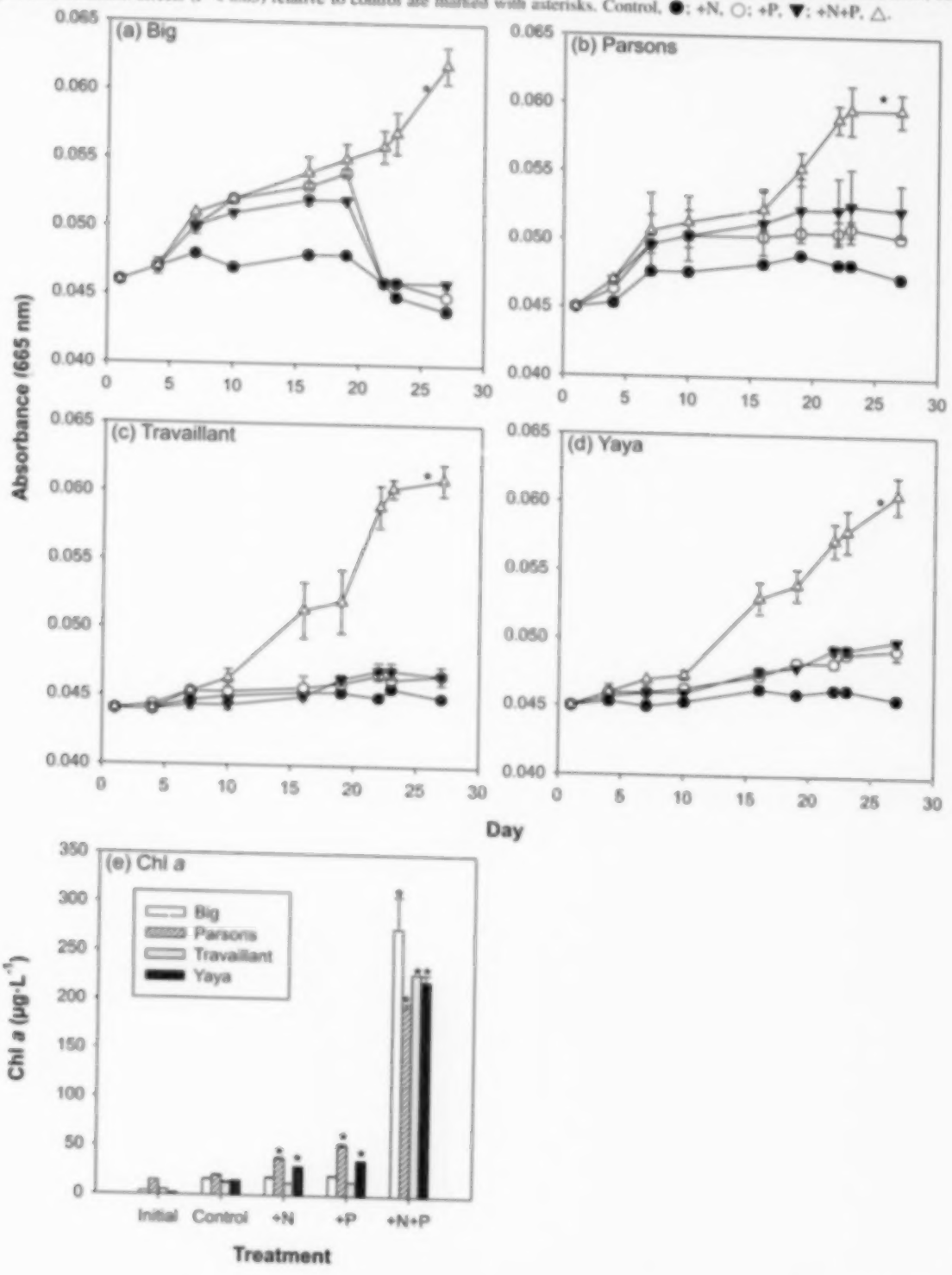
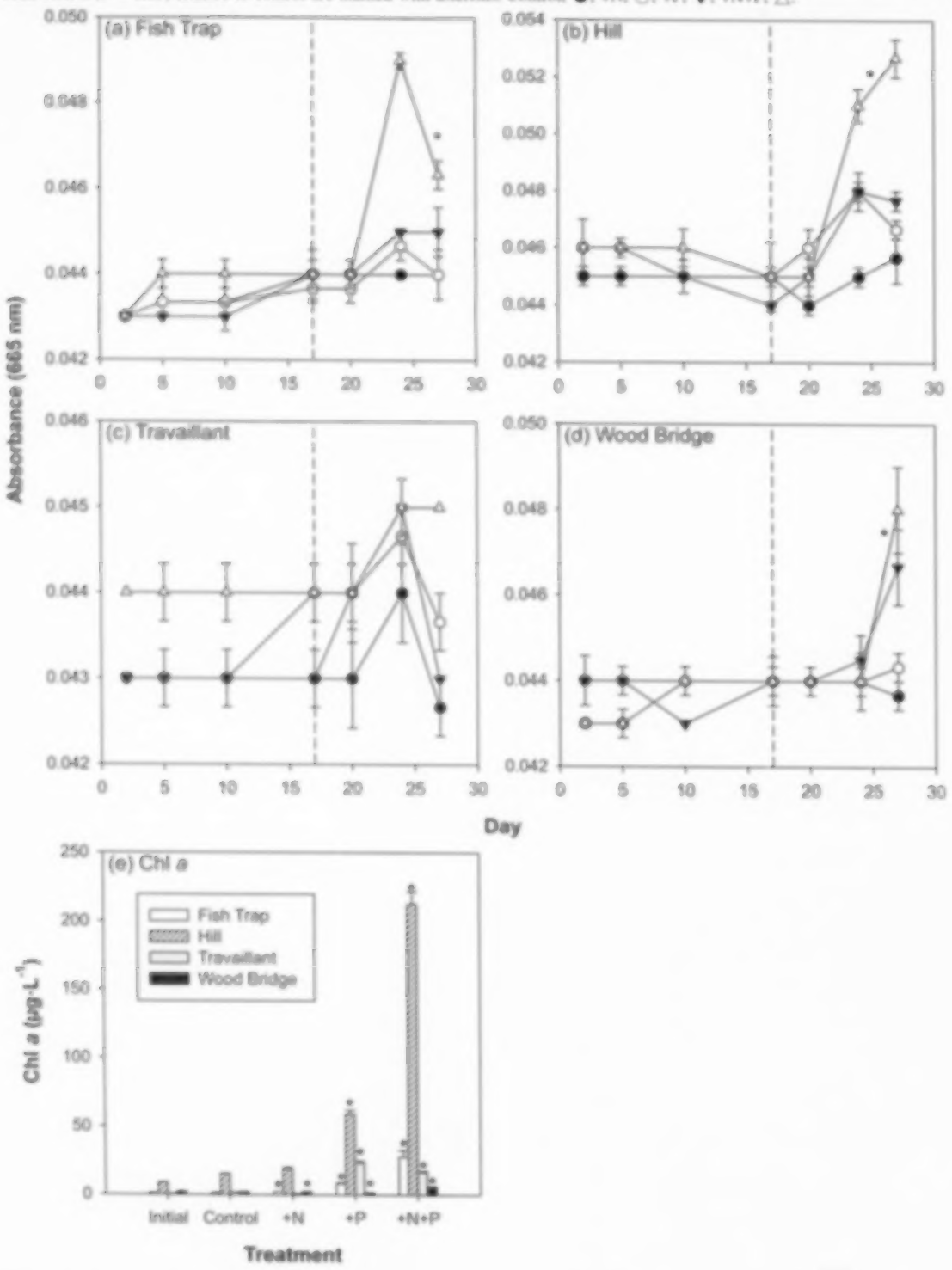


Fig. 6. Absorbance readings for winter (March 2007) nutrient enrichment bioassays: (*a*) Fish Trap Lake, (*b*) Hill Lake, (*c*) Travaillant Lake, (*d*) Wood Bridge Lake, and (*e*) Chl *a* concentrations from bioassays. Data are means of triplicate flasks (±1 standard error, SE). Significant treatment effects ($P < 0.05$) relative to control are marked with asterisks. Control, ●; +N, ○; +P, ▼; +N+P, △.



or season (winter versus summer). Several factors, not mutually exclusive, may help to explain this common pattern. First, most study lakes were shallow, where increased sediment–water interaction likely results in some nutrient regeneration from the sediments. Phytoplankton nutrient uptake rates here are likely keeping pace with regeneration rates, resulting in low levels of dissolved inorganic N and P. Another plausible explanation is that macrophytes, epiphytes, and benthic algae, which are abundant in these lakes, may be competing with phytoplankton for available nutrients (Squires et al. 2002; Squires and Lesack 2003; Ogbebo and Ochs 2008). Squires et al. (2002), for example, found that mean macrophyte biomass in Mackenzie River Delta lakes was high ($\sim$3000 g·m^{-2}). Similarly, benthic algae have been documented to contribute substantially to overall lake productivity in most oligotrophic systems (e.g., Sierszen et al. 2003 and references therein). Sierszen et al. (2003) found that the productivity in the food webs of two Alaskan Arctic lakes in the Toolik Lake region was mainly dominated by benthic production. In a related study, Bonilla et al. (2005) found a significant difference between the response of phytoplankton and that of benthic algae to nutrient enrichment. In that study, over 98% of phototrophic biomass in Ward Hunt Lake on Ward Hunt Island in the Canadian high Arctic occurred in the benthos, with benthic cyanobacteria dominant in these systems. They postulated that this trend might be prevalent in most high-latitude lakes because of the broad tolerance of benthic cyanobacteria to physical extremes.

Nitrogen and phosphorus co-limitation observed for Big, Yaya, (flooded) Noell, and Travaillant (nonflooded) lakes is similar to data reported for flooded and nonflooded Mackenzie River Delta and Tuktoyaktuk Peninsula lakes. In these lakes, sestonic C, N, P and chlorophyll ratios, alkaline phosphatase activity, and P and N debt indicated that phytoplankton communities here were most likely co-limited by N and P (Anema et al. 1990; Ramlal et al. 1991). Concurrent N and P limitation has also been documented for a variety of other Arctic and subarctic lakes, including Alaskan Arctic foothill (Levine and Whalen 2001), Canadian Shield (Healey and Hendzel 1980), as well as high Arctic lakes (Schindler et al. 1974; Douglas and Smol 2000; Bonilla et al. 2005). With regard to the flooded lakes of the above studies, the observation of N and P co-limitation contrasts sharply with the hypothesis that flooded lakes are largely light-limited as opposed to nutrient-limited (Fee et al. 1988). The lack of agreement with the hypothesis of Fee et al. (1988) may be a result of regular summer mixing in these shallow, flooded lakes. With mixing, phytoplankton are exposed to more sunlight and grow faster, thereby using (and depleting) more nutrients (Squires and Lesack 2002).

In this study, there was a lag of about 5 days before detectable responses to nutrient enrichment were observed. Such a lag period is common. A recent bioassay study conducted in Ward Hunt Lake in the Canadian Arctic demonstrated that differences in growth between nutrient-enriched and control treatments were only found after 15 days of incubation (Bonilla et al. 2005). Similarly, a close examination of algal bioassay plots from Little Manitou Lake in south-central Saskatchewan showed an 8-day lag period before significant response to nutrient addition was observed (Waiser and Robarts 1995). Studies have shown that nutrient-limited phytoplankton may temporarily decrease their photosynthetic activities in response to sudden nutrient addition (Lean and Pick 1981). The observed lag time, therefore, is physiologically needed so that algae can take advantage of the new nutrient conditions.

Although algal bioassays may overemphasize the importance of nutrient limitation while neglecting other potential limiting factors (e.g., light, temperature, nutrient resupply) and ignoring temporal dynamics or spatial variations in phytoplankton communities, they are still useful. They provide valuable information relevant to understanding and predicting effects of nutrient addition or removal (Elser et al. 1990; Ogbebo and Ochs 2008).

Limiting nutrients assessed from protein to carbohydrate ratio and N, P, and C ratios

To better assess phytoplankton nutrient status in the study lakes and to bolster the nutrient bioassay results, P and N deficiencies were further examined using protein to carbohydrate ratios, ambient TN:TP ratios, as well as particulate N, P, and C ratios. These ratios provide integrated, weighted measures of phytoplankton nutritional status over longer time scales (Smith 1982; Davies et al. 2004). Protein to carbohydrate ratios (<0.7) recorded in this study indicate that phytoplankton communities in the lower MRB are severely limited by nutrients (cf. Pick 1987). These results clearly support conclusions drawn not only from the bioassays but from the low ambient dissolved inorganic nutrient concentrations observed in most of the study lakes.

The TN:TP ratios from most of the study lakes were >17, indicating general P deficiency. In oligotrophic lakes, like the ones in this study, high TN:TP ratios tend to prevail because of a reliance on catchment inputs that typically export more N than P (Downing and McCauley 1992). Additionally, in lakes with TP concentrations $\leq$ 50 µg·L^{-1}, TN:TP ratios $\leq$ 10 (nitrogen limitation) are generally not seen. The finding of P deficiency is in agreement with an empirical analysis of algal biomass from 433 lake-years that suggested that Arctic lakes generally had TN:TP ratios greater than 14 (Flanagan et al. 2003). While this evidence would suggest that most Arctic or subarctic lakes are most likely P-limited, studies conducted in Toolik Lake revealed N rather than P limitation (Levine and Whalen 2001). Nitrogen limitation has been attributed to the high P-adsorbing capacity of lake sediments in this region (Levine and Whalen 2001). Nitrogen deficiency has also been reported for many lakes and ponds located in Melville Island, high Arctic Canada (Keatley et al. 2007).

Phytoplankton cellular nutrient content often approximates the Redfield C:N:P (molar) ratio of 106:16:1 when growing at or close to maximum rates (Redfield 1958). Consequently, deviations from this ratio are used to infer N or P deficiency. According to the Redfield criteria, sestonic ratios derived from our study lakes suggest P but not N limitation. This result tends to mirror results obtained from the TN:TP ratios, but not those from the bioassays. The explanation may lie in the fact that sestonic protein to carbohydrate ratios and TN:TP ratios represent nutrient deficiency over a longer time scale than the bioassays. Further seasonal work, using more sensitive physiological tests, like ^{32}P uptake and

turnover times, could indicate which nutrient(s) is (are) limiting and if limitation changes on a seasonal basis. Taken together, although nutrient and sestonic ratios do not completely agree with the bioassay results, they emphasize the relative importance of P rather than N in controlling algal growth in the study lakes.

Temperature effects on algal growth

Nutrients are not the only factors controlling phytoplankton growth in cold Arctic and subarctic lakes. It has been suggested that physical factors such as ice cover, light, and temperature may be equally important. In Arctic lakes, for example, algal biomass has been shown to increase at a lower rate for a given increase in P than that of warmer temperate lakes (Flanagan et al. 2003). In fact, low temperatures may actually suppress algal growth rates to the extent that available nutrients are not fully utilized (Riegman and Mur 1986). The effect of temperature, as another prominent factor determining phytoplankton biomass, was clearly demonstrated in the March 2007 experiment. For the first 17 days of this experiment, there was no significant difference ($P < 0.05$) in absorbance between differing nutrient treatments (+N, +P, or +N+P) relative to the control. Following an increase in temperature from 6 to 10 °C, however, absorbance significantly increased (especially in the +N+P treatment). A similar observation was made in situ at Hill Lake where despite relatively high nutrient levels, Chl *a* concentrations were considerably lower for March compared with summer values. Similar differences between winter and summer periods could be inferred for Travaillant, Wood Bridge, and Fish Trap lakes.

In conclusion, results presented here clearly show that simultaneous addition of N and P dramatically enhanced growth in all study lakes of the lower MRB irrespective of watershed and flooding type, with substantially lower growth with N or P additions alone. Anthropogenic disturbances that result in simultaneous N and P additions likely will increase algal growth and may even alter the trophic status of these northern lakes (cf. Michelutti et al. 2003). Increased nutrient and organic matter release into lakes, in turn, could decrease oxygen concentration especially during winter or in deep stratified lakes such as Yaya. Global warming may also enhance productivity rates through direct temperature effects and through increased N and P inputs from the watershed (e.g., with permafrost melt; Smith et al. 2005; Smol et al. 2005). From a management perspective, close attention must be paid to the potential interacting effects of ongoing rapid development and global warming.

Our studies have utilized a broad survey approach to characterize limnological conditions in a wide variety of lakes along the pipeline route and to refine scientific and management questions. Based on our findings, the next focus of limnological research should be on investigating phytoplankton nutrient recycling and competition with macrophytes as well as nutrient regeneration from bottom sediments (i.e., to clarify mechanisms regulating nutrient regeneration from bottom sediments versus uptake rates in these sites). These more in-depth, process-oriented studies should be conducted at a subset of these lakes, with Parsons, Big, Yaya, and Travaillant lakes being particularly good candidates for investigating ecosystem change due to anthropogenic disturbances (including drill pad and pipeline development) and climate change. The ultimate goal for research in this region is to acquire adequate baseline data for evaluating changes in aquatic ecosystems that may result from future human development and global warming.

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Estimating establishment probabilities of Cladocera introduced at low density: an evaluation of the proposed ballast water discharge standards

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Abstract: The International Maritime Organization has proposed ballast water discharge standards to reduce densities of taxa transported in ballast water. While reduced propagule pressure will almost certainly lower the risk of species introductions, we ask if the proposed standards will be effective against taxa capable of rapid population growth from small inocula, such as parthenogenetic taxa. We modified a diffusion approximation to calculate establishment probabilities as the probability of reaching a critical threshold density necessary to initiate sexual reproduction (and production of diapausing eggs for long-term persistence) before the onset of adverse environmental conditions. We parameterize our model for six Cladocera using growth rates measured during enclosure experiments conducted under favourable environmental conditions (i.e., using a precautionary approach). We then examine predicted establishment probabilities at different inoculum densities to determine the efficacy of the proposed ballast water discharge standards. Our results indicate that future technologies in compliance with the proposed standards could reduce establishment probabilities for some parthenogenetic zooplankton threefold; however, there is still a risk of establishment for some taxa.

Résumé : L'organisation maritime internationale a proposé des normes concernant l'évacuation de l'eau de ballastage afin de réduire la densité des taxons transportés dans cette eau de ballastage. Bien qu'une pression réduite des propagules puisse diminuer presque certainement le risque d'introduction d'espèces, nous nous demandons si les normes proposées seront efficaces contre les taxons capables d'une croissance rapide de population à partir de petits inoculums, comme les taxons parthénogénétiques. Nous avons modifié une approximation de la diffusion afin de calculer la probabilité d'établissement définie comme étant la probabilité d'atteindre la densité seuil requise pour l'initiation de la reproduction sexuelle (et la production d'œufs de diapause pour la persistance à long terme) avant l'arrivée de conditions environnementales défavorables. Nous avons déterminé les paramètres du modèle pour six cladocères en utilisant des taux de croissances mesurés dans des expériences en enclos menées dans des conditions favorables de milieu (donc en utilisant une approche prudente). Nous avons ensuite examiné les probabilités d'établissement prédites à diverses densités d'inoculum afin de déterminer l'efficacité des normes proposées pour l'évacuation de l'eau de ballastage. Nos résultats indiquent que des technologies futures en accord avec les normes proposées pourraient réduire par un facteur de trois les probabilités d'établissement de certains organismes parthénogénétiques du zooplancton; il demeure encore, néanmoins, un risque d'établissement pour certains taxons.

[Traduit par la Rédaction]

Introduction

At least 1000 nonindigenous species have been reported from aquatic habitats globally (e.g., Leppäkoski et al. 2002; Hayes and Sliwa 2003; Ricciardi 2006), with ballast water recognized as the primary vector of unintentional aquatic introductions (Carlton 1985; Ruiz et al. 1997, 2000). Although regulations requiring vessels to exchange low-salinity or coastal ballast water for midocean saltwater were put into place for the Laurentian Great Lakes nearly 20 years ago, the rate of invasion does not appear to have decreased (Ricciardi 2006; but see Costello et al. 2007). As a result, there has been increased public pressure to develop alternative treatment technologies. The International Maritime Organization (IMO) proposed minimum discharge standards that must be met for any technology to receive international approval, including a standard applicable to zooplankton (<10 individuals greater than 50 μm in minimum dimension per

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cubic metre, summed over *all* species (International Maritime Organization 2004)). While this standard is approximately 10 times lower than densities typical of exchanged ballast water (Minton et al. 2005), it is a nonzero value, and the resultant efficacy has not been empirically examined.

Predicting probabilities of establishment is a complex task, even with a prescribed level of propagule pressure (see Jerde and Lewis 2007). We suggest that it is important to evaluate the proposed standard under a worst-case scenario; that is, how effective will the standard be for taxa capable of rapid population growth following introduction of only a few individuals into a suitable habitat? Cyclically parthenogenetic zooplankton are of particular concern in the Great Lakes region, comprising five of the 26 invertebrate invaders reportedly introduced via ballast water since 1959 (Ricciardi 2006). Cyclical parthenogenesis maximizes population growth rate under favourable environmental conditions via asexual reproduction, while long-term population persistence through unfavourable environmental conditions (i.e., establishment) is achieved via sexually produced diapausing eggs (Dodson and Frey 2001). The parthenogenetic production of males, and subsequent production of diapausing eggs, seems to be primarily induced by crowding and a shortening of the photoperiod in temperate regions (Carvalho and Hughes 1983; Hobaek and Larsson 1990; Larsson 1991). Thus, determining the probability of reaching the critical threshold density necessary to induce parthenogenetic production of males, while photoperiod and other environmental conditions are still appropriate, will be crucial for estimating establishment probabilities of parthenogenetic taxa in temperate waters.

To model establishment probabilities for parthenogenetic taxa, we modified an existing diffusion approximation (Whitmore and Seshadri 1987; Lande and Orzack 1988) to calculate the probability of reaching a critical threshold density at any point between propagule introduction and the onset of adverse environmental conditions. We parameterize our model for six Cladocera using growth rates measured during enclosure experiments conducted under favourable environmental conditions (i.e., using a precautionary approach, since physical, chemical, and biological factors limiting establishment success are minimized). We then examine predicted establishment probabilities at different inoculum densities to determine the efficacy of the proposed ballast water discharge standards in comparison with ballast water exchange. Finally, to generalize our results, we test the hypothesis that establishment probabilities are greatest for species with the highest stochastic population growth rates.

Materials and methods

Modelling approach

Stochastic models of population growth have been used to estimate probabilities of establishment as the complement of the probability of extinction (Haccou and Iwasa 1996; Drake 2004; Drake et al. 2006). This method indirectly depends on the threshold population size used to estimate extinction or quasi-extinction (see Morris and Doak 2002). For parthenogenetic taxa, extinction thresholds have been defined as zero individuals, since a single individual could theoretically generate an exponentially growing population. As a result, computation of probabilities of establishment as the complement of extinction probabilities could be uninformative when probabilities of extinction close to zero generate probabilities of establishment close to one (e.g., Drake et al. 2006). Thus, we model the probability of establishment using a variant of a diffusion approximation originally developed to calculate the probability of extinction at any point between the present and a specified future time point (Whitmore and Seshadri 1987; Lande and Orzack 1988). We modified the original model to calculate establishment probability as the probability of reaching a critical reproductive threshold density (critical for the onset of sexual reproduction and formation of diapausing eggs) at any point between propagule introduction and the onset of adverse environmental conditions (see below). This framework is particularly appropriate for estimating establishment probabilities for Cladocera in temperate environments where production of diapausing eggs is a requisite for long-term population persistence.

We used six taxa with ubiquitous occurrence in Hamilton Harbour, Lake Ontario, as "model" Cladocera: *Bosmina* (*Eubosmina*) *coregoni* Baird, *Bosmina* spp. exclusive of *Bosmina coregoni*, *Ceriodaphnia lacustris* Birge, *Chydorus sphaericus* (O.F. Müller), *Daphnia retrocurva* Forbes, and *Daphnia galeata* Sars *mendotae* Birge. Establishment probabilities were determined for each species using two steps: (*i*) computation of critical reproductive threshold densities predicted from allometric models based on body size and (*ii*) estimation of the probability of reaching the species-specific critical threshold density from the diffusion approximation using stochastic population growth rates obtained from low density populations inside enclosures and high density populations in the surrounding natural environment. To evaluate the efficacy of the proposed ballast water discharge standards, we then examined the effect of inoculum density on establishment probabilities.

Critical reproductive threshold densities

Population density is one of many factors acting in combination to induce a change in reproductive mode from parthenogenesis to gamogenesis in zooplankton populations (e.g., Kleiven et al. 1992, and references therein). While multiple factors are involved, cues such as food availability or day-length changes will be irrelevant if population density is below the minimum critical threshold density. Because of challenges involved in the separation of different density-dependent factors, few studies have empirically determined critical densities necessary to induce the switch in reproductive strategy; however, Carvalho and Hughes (1983) experimentally determined that critical densities of *Daphnia magna* Straus ranged from 3×10^5 to 4×10^5 individuals·m^{-3} (see also Rose et al. 2002). Given that the number of individuals required to establish a viable population is predicted to be inversely proportional to body size (Drake et al. 2005), we parsimoniously estimated critical reproductive threshold densities for each of the six study species (C_i, individuals·m^{-3}) from the proportionality between body size and critical density observed in *D. magna*. The allometric relationship between body size (W, kg fresh mass) and density at carrying capacity (D, individuals·km^{-2}) developed for aquatic invertebrates by Peters and Wassenberg (1983) was

used to determine saturation densities for the six cladoceran species in our study and for the reference species *D. magna*:

$$(1) \quad \log_{10} D = 5.37 - 0.58 \log_{10} W$$

The C_i value for species i was then estimated using the relationship between adult body size and the C value in *Daphnia magna* Straus as a reference:

$$(2) \quad C_i = D_i C_R D_R^{-1}$$

where D_i is the species' allometric density as computed from eq. 1, C_R is the critical reproductive threshold density of the reference species, and D_R is the allometric density of the reference species.

Average adult weights of five of the study species were estimated from measurements previously recorded from samples taken in Hamilton Harbour in 2004 (O.E. Johannsson and K.L. Bowen, unpublished data). As data for *Ceriodaphnia lacustris* was insufficient, its average body weight was estimated from an interspecific logarithmic regression of weight (W; in μg) on length (L; in μm) across the 384 individuals of Cladocera measured in 2004 ($\log_e W = 1.7909 \log_e L - 10.969$; $r^2 = 0.86$; $p < 0.001$) using the adult length of *Ceriodaphnia reticulata* (Jurine) (0.56 mm; Gliwicz and Umana 1994). This regression was also used to estimate the average weight of adult *D. magna* from its length at maturity (2.24 mm; Gliwicz and Umana 1994). Two critical reproductive threshold densities were generated for each species based on the low and high C_R values experimentally determined for *D. magna* by Carvalho and Hughes (1983).

Diffusion approximation

Commonly used to estimate extinction probabilities of structured and nonstructured populations (Dennis et al. 1991; Orzack 1997), the diffusion approximation combines population dynamics with probability theory. Not to be confused with the physical dispersal of individuals, the term diffusion refers to the fact that the model considers the changing normal distribution of log population size as a cloud of particles undergoing diffusion with drift (Morris and Doak 2002). This stochastic cloud is defined by the infinitesimal mean (μ) and variance (σ^2) of the probability distribution of the logarithm of population size. While values of μ and σ^2 are derived from intrinsic rates of growth (r) between sampling intervals, the probability estimates generated with the diffusion approximation are not a direct extrapolation of deterministic growth rates. The diffusion approximation (1) implies that changes in the logarithm of population size are temporally independent and normally distributed; (2) assumes density-independent environmental stochasticity; and (3) does not account for demographic stochasticity in the analysis (Dennis et al. 1991). Regarding point 1, the asymptotic lognormality of population growth is usually a good predictor of changes in population size (Tuljapurkar and Orzack 1980), and any violation of these assumptions are revealed by resampling simulations (Lande and Orzack 1988), which we incorporate later in our analysis. Orzack (1997) demonstrated that the diffusion approximation adequately describes the dynamics of density-dependent populations. As demographic stochasticity, ascribed to the probability of mating, is not an issue in our application of the diffusion analysis to probabilities of establishment in parthenogenetic taxa, we are confident in our application of the model. We do note, however, that demographic stochasticity associated with survival probabilities occurs even in asexual species at low densities (Lande 1993).

Model structure

We used a diffusion approximation with an inverse Gaussian distribution to calculate the probability density (g) of reaching the critical reproductive threshold density in a small segment of time (t):

$$(3) \quad g(t|\mu, \sigma^2, d) = \frac{d}{\sqrt{2\pi\sigma^2 t^3}} \exp\left[\frac{-(d+\mu t)^2}{2\sigma^2 t}\right]$$

where d is the difference between the log of C and the log of the inoculum density (D_0) (i.e., $d = \log C - \log D_0$), and μ and σ^2 are the mean and variance of log population growth in which day-to-day variation in population growth rate can be expressed as probabilities in a stochastic process. Mean log population growth (μ) and its variance (σ^2) were obtained from time-series counts in enclosure experiments and natural populations using the approach of Dennis et al. (1991), which accounts for gaps or irregularities in sampling intervals (see next section for design and sampling methodology for enclosure and natural populations). This procedure involves regressing $\log(N_{i+1}/N_i)/(t_{i+1} - t_i)^{1/2}$ on $(t_{i+1} - t_i)^{1/2}$ forcing the intercept to zero, where N is the mean population size across replicates, and i and $i + 1$ define the sampling interval (i.e., the transition). Mean log population growth (μ) is then estimated from the slope of this regression and σ^2 from the regression mean square error. The lack of temporal autocorrelation required by this method was evaluated from residual analysis using the Durbin–Watson statistic.

Estimates of σ^2 were corrected for observation error caused by using counts representing means of replicate samples. The information contained in the variance of each day's samples was used to compute the mean variance in log population growth (V, to distinguish from σ^2) caused by sampling variation:

$$(4) \quad V = \frac{1}{q}\sum_{t=1}^{q}\left[\left(\frac{s_t^2}{n_t N_t^2}\right) + \left(\frac{s_{t+1}^2}{n_{t+1} N_{t+1}^2}\right)\right]$$

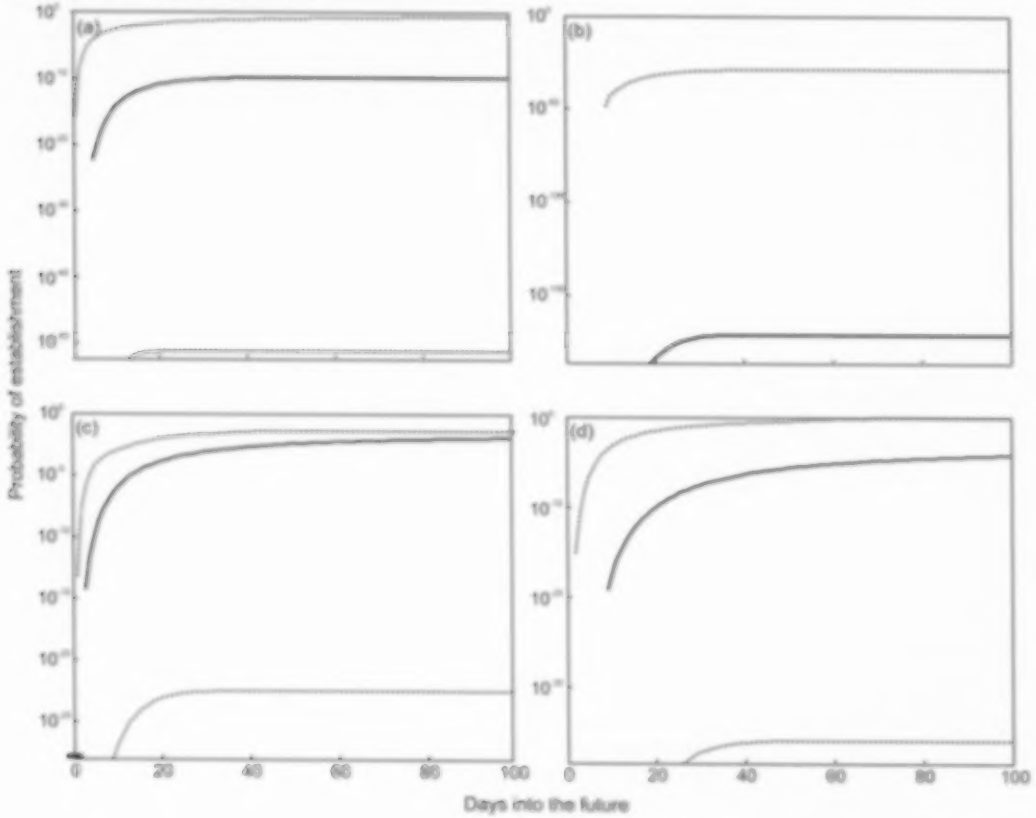
where s_t is the standard deviation of the n_t replicates used to compute N_t (Morris and Doak 2002), and q is the total number of transitions (time intervals used to estimate population growth) in the data set (Dennis et al. 1991). A corrected estimate of σ^2 was then computed as $\sigma_c^2 = \sigma^2 - V$.

The integration of eq. 3 from time t to a specific time horizon (T) results in the cumulative distribution function:

$$(5) \quad G(T|d, \mu, \sigma^2) = \Phi\left(\frac{-d - \mu T}{\sqrt{\sigma^2 T}}\right) + \exp\left(\frac{-2\mu d}{\sigma^2}\right)\Phi\left(\frac{-d + \mu T}{\sqrt{\sigma^2 T}}\right)$$

where $\Phi(y)$ is the standard normal distribution:

Fig. 1. Typical response curves (solid line: best estimate; broken lines: upper and lower bounds of the 95% confidence interval) for the probabilities of establishment of cladoceran populations as a function of time (days into the future) and low critical reproductive threshold density (C_L). Projections are depicted for enclosure and natural populations of *Daphnia retrocurva* (*a*, *c*) and *Daphnia galeata mendotae* (*b*, *d*), respectively, given inoculum densities of 10 individuals·m^{-3}. These two species were chosen to exemplify projection curves, as they represent the species with highest (*D. retrocurva*) and lowest (*D. galeata*) probabilities of establishment. Note differences in the scale of the *y* axes both between species and environments.



$$\Phi(y) = (1/\sqrt{2\pi}) \int_{-\infty}^{y} \exp(-z^2/2)dz \quad (6)$$

Finally, to account for uncertainty in the estimates of μ and σ^2, we used a parametric bootstrap with 2500 iterations to approximate 95% confidence intervals (CIs) for probabilities of establishment. Mean log population growth (μ) was drawn from a lognormal distribution and σ^2 from the distribution of a χ^2 random variable multiplied by σ^2/q. CIs for μ and σ^2 were obtained as described by Dennis et al. (1991), with $(\mu - \tau_{0.05,q-1}\mathrm{SE}[\mu], \mu + \tau_{0.05,q-1}\mathrm{SE}[\mu])$ defining the 95% CI for μ, and $([q-1]\sigma^2/\chi^2_{0.025,q-1}, [q-1]\sigma^2/\chi^2_{0.975,q-1})$ the 95% CI for σ^2, where $\tau_{0.05,q-1}$ is the critical value of the two-tailed Student distribution, SE is the standard error of the slope in the regression, and $\chi^2_{\alpha/2,q-1}$ is the critical value of the χ^2 distribution.

We chose a time horizon of 100 days in the future, since our preliminary results indicated that the probability of establishment quickly approaches an asymptotic value (within 40 days, see Fig. 1; similar results are reported for other Cladocera by Drake et al. 2006). This timeframe is more than sufficient to allow establishment probabilities to reach asymptotic values while being biologically meaningful, since the studied taxa are typically recorded from the water column for 140–170 days each year (O.E. Johannsson and K.L. Bowen, unpublished data).

The methodology outlined above was first completed for each of the six study species using data generated from natural populations external to enclosures to test the appropriateness of the model; probabilities of establishment for natural populations were expected to be close to 1 for densities observed at the final time point in the series and perhaps even for lower densities. Subsequently, the model was run with independent data from enclosure populations. We applied this procedure at both C values computed for each species, thereby generating six outcomes for the diffusion approximation (eq. 5) for the cumulative probability of establishment at 100 days in the future for each habitat type: $(P(E_{\mathrm{best,\ high}}))$, $(P(E_{\mathrm{upper,\ high}}))$, $(P(E_{\mathrm{lower,\ high}}))$, $(P(E_{\mathrm{best,\ low}}))$, $(P(E_{\mathrm{upper,\ low}}))$, and $(P(E_{\mathrm{lower,\ low}}))$, where the subscripts denote that the estimate is based on the trajectory of the best

fit, upper or lower 95% CI, and the high or low critical reproductive threshold limit.

Enclosure experiments

Two enclosure experiments were conducted in 2006 within the basin of Pier 9 in Hamilton Harbour, Lake Ontario (43°16′31.82″N, 79°51′12.19″W). The location was selected for its proximity to shipping activity (potential ballast discharge site in the Great Lakes) and because it was a private, relatively sheltered area of the harbour where physical damage to enclosures would be minimized. Enclosures were constructed and sampled following the methodology of Arnott and Vanni (1993). Briefly, 6 mL polyethylene bags, 1.5 m in diameter and ~3.5 m deep (~5000 L), were suspended from floating wooden frames in sets of four. Enclosure openings were raised 30 cm above the water surface and covered with polyethylene tarps stretched across the top of the framing (leaving 10 cm air space between tarps and enclosures). Two experiments were run, beginning 27 July and 4 August, respectively, with each experiment consisting of 16 replicate enclosures. Harbour water drawn from 3 m depth was pumped into enclosures through a consecutive series of filters (110, 73, 53 μm) in an attempt to preclude all Cladocera from enclosures. This filtration methodology proved to be problematic because of high concentrations of algae and particulate matter in the harbour water. As a result, 10 net hauls (50 cm diameter, 64 μm mesh conical plankton net) were conducted in each replicate to further reduce plankton densities prior to inoculation with known cladoceran communities collected from the adjacent harbour water.

While we inoculated Cladocera at levels near the proposed ballast water discharge standard (i.e., 10 individuals·m^{-3}), we suspected that viable parthenogenetic eggs may have been forced through the filters into enclosures. As parthenogenetic eggs of Cladocera typically hatch within 3–4 days at 20 °C (Gillooly 2000), we were concerned that hatching of any such eggs would augment population densities, resulting in artificially inflated growth rates at the onset of the experiments. As a result, enclosures were left to equilibrate for 4 days before experiments commenced (i.e., time 0 of the experiment occurred 4 days after enclosures were set up). While this method limited the ability to achieve densities of 10 individuals·m^{-3} at the onset of the study, it was the only way to minimize the overestimation of growth rates in the first few days of the experiments.

Zooplankton were sampled twice weekly at the same time of day using a 30 cm diameter, 100 μm mesh conical plankton net. One net haul, 3.5 m in depth, was retrieved at a speed of 0.5 m·s^{-1} near the centre of each bag, sampling ~5% of the total volume. Analyses of additional vertical and horizontal sweep samples collected along the edges of the enclosures indicated that there was no sampling bias due to "edge effects" (i.e., increased density of herbivorous zooplankton near enclosure walls). A correction factor was applied to zooplankton densities after measurement of plankton net efficiency (see Arnott and Vanni 1993) and vertical migration of plankton inside bags (as revealed by net hauls collected during daylight and midnight hours); the application of this correction factor did not affect results of later estimates of establishment probabilities.

Collected samples were preserved in 4% buffered sugar formalin for later analyses. Abiotic water-quality parameters (temperature, pH, conductivity, salinity, and dissolved oxygen) were measured in each bag prior to net hauls using a Hydrolab Datasonde 4a. All equipment was rinsed with tap water between bags to prevent transfer of animals between bags. On each sampling date, three additional net hauls and four Hydrolab readings (3.5 m in depth) were collected along a 16 m transect directly parallel to the enclosures to monitor natural zooplankton communities and ambient abiotic conditions external to the enclosures. After a cumulative loss of eight and six replicates because of wave stress, the experiments were terminated on August 18 and 21, resulting in six and five time-series growth measurements for the first and second experiments, respectively. Separate repeated measures analysis of variance (RM-ANOVA) were used to test for differences between the abiotic water-quality parameters measured in enclosures and the ambient environment across time. Parameter values were log-transformed prior to analysis to improve normality and homoscedasticity.

Samples collected at time 0 were examined in their entirety. All subsequent sample collections were examined using a stratified counting regime modified after Cooley et al. (1986). Each sample was diluted to a known volume, with subsamples drawn at random using a 5 mL Henson–Stempel pipette. At least 500 individuals were enumerated to estimate abundances of dominant taxa; additional subsamples representing at least 7% of the sample volume were drawn to enumerate subdominant taxa.

Effective inoculum density

Since probabilities of establishment are partly determined by inoculum size, we examined model predictions produced at a range of inoculum densities (D_0), from 10 individuals·m^{-3} to 10% of the critical reproductive threshold density ($0.1C_r$). This covers the range of densities feasible for zooplankton in ballast water (i.e., from the proposed IMO discharge standard to densities reported from untreated ballast water). This range is also dictated by the limitations of the methodology, as it is not advisable to generate probabilities of establishment for population densities greater than $0.1C_r$ because finite-time establishment probabilities will be predicted inaccurately as the difference between D_0 and D_r diminishes (see Orzack 1997). Comparison of the probability of establishment at an inoculum density of 10 individuals·m^{-3} with that of 100 individuals·m^{-3} is of particular interest, as it is consistent with the expected efficacy of the proposed IMO discharge standard for ballast water treatment compared with the status quo (ballast water exchange). As it is unlikely that discharged ballast will consist entirely of a single species of parthenogenetic taxa (e.g., Duggan et al. 2005), we also examined establishment probabilities for inocula below 10 individuals·m^{-3}.

Results

Population parameters

Inoculum densities in enclosures (as measured at time 0) were generally one to two orders of magnitude lower than natural population densities external to enclosures, ranging from <10 to nearly 400 individuals·m^{-3} for each taxon

(Table 1). Analysis of population trends for the experimental period indicated that most low density populations inside enclosures were undergoing exponential growth, while most high density natural populations were not (Fig. 2). In addition, density variation increased with experimental day in enclosures but remained relatively stable in natural populations. At the termination of the experiments, all enclosure populations had substantially increased in size, with populations of *Bosmina* spp. and *D. galeata mendotae* exceeding densities in the natural environment. Both natural and enclosure populations exhibited positive μ values over the time series, with enclosure populations exhibiting higher μ values than natural populations (Table 2). With the exception of *D. retrocurva*, the 95% lower bound of the CI for μ was also positive for all enclosure populations and negative for all natural populations. The long-term dynamics of all studied populations were also characterized by large variance (σ^2). While values of σ^2 were very high for some species, they were substantially greater for natural populations than for enclosures. The analysis of residuals through the Durbin–Watson statistic did not detect any significant autocorrelation in growth rates of any time series, indicating that application of the diffusion approximation is appropriate.

Analysis of abiotic conditions

Environmental conditions in enclosures were very similar to the ambient environment (Fig. 3). Minor, but statistically significant, differences (RM-ANOVA, $p < 0.05$) were observed for conductivity and salinity in both experiments and for dissolved oxygen in the first experiment. These differences are a result of the extremely low variability measured in these parameters, and we suggest that although statistically significant, these differences are not biologically meaningful, since the magnitude of difference between enclosures and the ambient environment was typically an order of magnitude smaller than that observed within each habitat type between sampling dates.

Probabilities of establishment

Establishment probabilities for all study species rapidly approached asymptotic values over time in both enclosure and natural populations. Projected curves began to flatten after a few weeks for inoculum densities as low as 10 individuals·m^{-3} (Fig. 1), while asymptotic values were reached after approximately 10 days for inoculum densities equal to 10% of the critical reproductive threshold densities (data not shown). Generally, as inoculum density increases, the rate at which asymptotic establishment probabilities are reached also increases. CIs for establishment probabilities were wide for all species studied, but were wider for populations in enclosures than for those in the natural environment. The wide CIs reflect the range of observed variability associated with establishment probabilities given the dynamics inferred from the time-series data collected from enclosure and natural populations.

Our diffusion approximation estimated probabilities of establishment of 1 for all natural populations at the densities observed at the end of the experimental period, confirming that the results of the diffusion model applied here are within reason, as taxa with resident populations in the harbour are expected to exhibit robust probabilities of establish-

Table 1. Mean (± standard error, SE) cladoceran densities (individuals·m^{-3}) in enclosure (upper value) and natural (lower value) populations at the onset and termination of experiments and estimated critical reproductive threshold values (*C*) by species.

	Experiment No. 1		Experiment No. 2		Critical density (*C*)	
Taxon	Initial density	Final density	Initial density	Final density	Low	High
Bosmina coregoni	96 (29)	21 392 (4 983)	110 (35)	10 436 (2 200)	1 101 158	1 468 210
	1 377 (79)	19 554 (2 448)	5 078 (722)	22 777 (1 866)		
Bosmina spp.	412 (119)	136 254 (31 070)	375 (122)	184 705 (30 139)	1 555 336	2 073 781
	3 726 (578)	10 412 (529)	35 885 (6 999)	124 637 (33 086)		
Ceriodaphnia lacustris	4 (2)	509 (173)	8 (3)	362 (74)	1 266 176	1 688 235
	116 (27)	696 (122)	665 (27)	2 171 (648)		
Chydorus sphaericus	18 (6)	5 923 (3 631)	42 (12)	744 (218)	2 305 318	3 073 757
	17 602 (1 293)	42 765 (3 998)	23 614 (2 565)	21 754 (1 514)		
Daphnia galeata mendotae	12 (6)	4 890 (2 318)	8 (4)	404 (238)	600 078	800 104
	253 (36)	1 016 (105)	322 (37)	1 041 (139)		
Daphnia retrocurva	4 (2)	3 398 (1 555)	22 (4)	2 027 (433)	720 146	960 194
	7 688 (507)	135 607 (27 175)	3 266 (682)	54 726 (3 612)		

Note: Mean population densities are calculated from 9, 8, and 3 replicates for enclosure experiments 1 and 2 and natural harbour samples, respectively.

Fig. 2. Mean (± standard error, SE) number of individuals·m^{-3} by day for (*a*) *Bosmina* spp., (*b*) *Daphnia retrocurva*, (*c*) *Chydorus sphaericus*, (*d*) *Bosmina coregoni*, (*e*) *Ceriodaphnia lacustris*, and (*f*) *Daphnia galeata mendotae* from the first experiment. Solid and open circles denote data from enclosures and ambient harbour water, respectively. Note differences in the scale of the y axes for each panel.

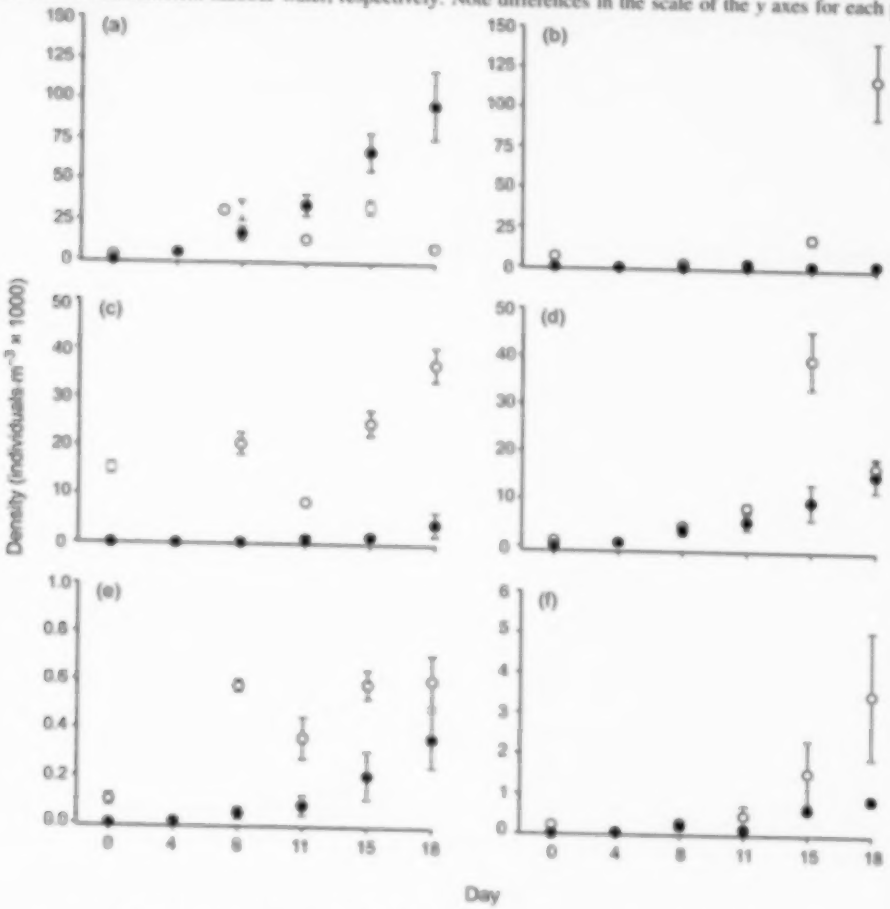
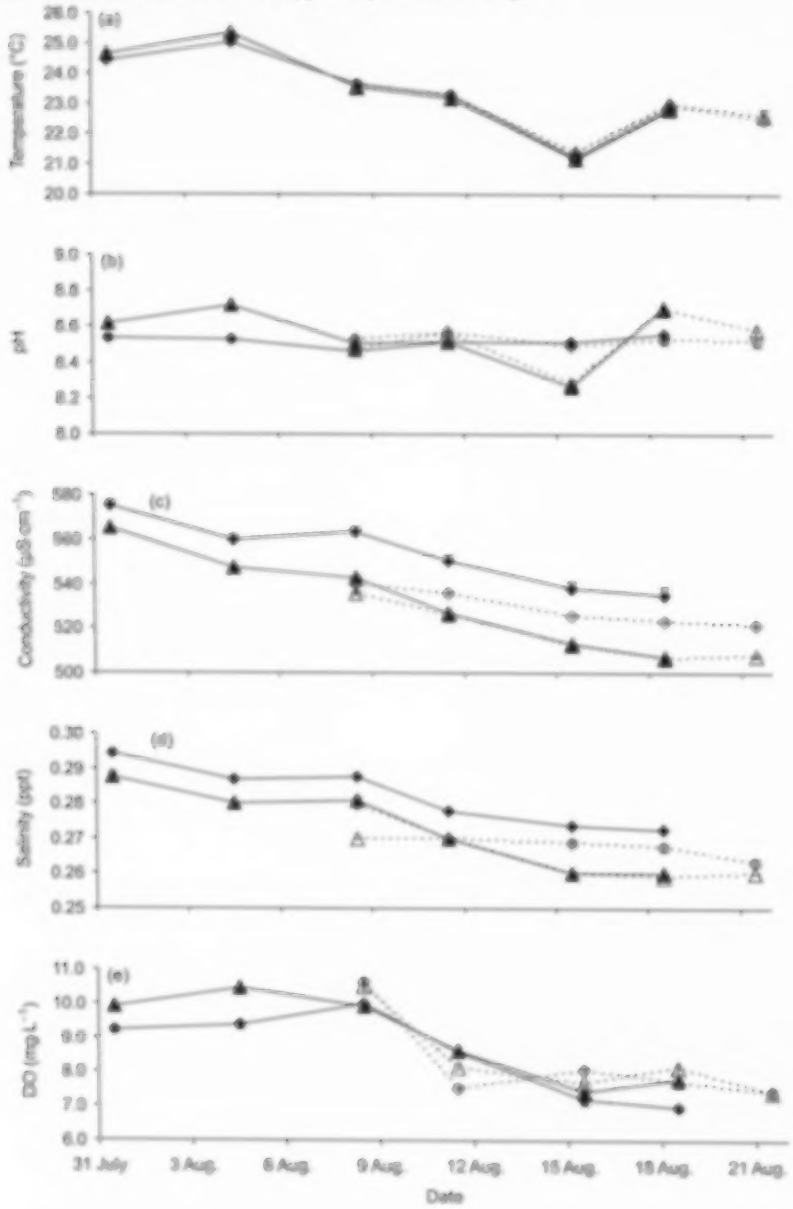


Table 2. Mean population growth rate (μ) and associated variance (σ^2), with lower and upper bounds of 95% confidence intervals for enclosure (upper value) and natural (lower value) populations, by species.

	μ			σ^2		
Species	Lower bound	Mean	Upper bound	Lower bound	Mean	Upper bound
Bosmina coregoni	0.031	0.302	0.572	0.061	0.171	1.409
	−0.141	0.134	0.409	0.074	0.206	1.701
Bosmina spp.	0.021	0.322	0.623	0.076	0.211	1.746
	−0.367	0.167	0.702	0.279	0.778	6.427
Ceriodaphnia lacustris	0.167	0.250	0.334	0.006	0.016	0.132
	−0.082	0.139	0.361	0.048	0.134	1.106
Chydorus sphaericus	0.141	0.321	0.502	0.027	0.076	0.628
	−0.254	0.010	0.274	0.068	0.190	1.568
Daphnia galeata mendotae	0.242	0.331	0.420	0.007	0.019	0.153
	−0.191	0.067	0.326	0.065	0.182	1.500
Daphnia retrocurva	−0.038	0.344	0.725	0.122	0.339	2.802
	−0.354	0.093	0.541	0.196	0.547	4.513

Fig. 3. Mean (± standard error, SE) values of (*a*) temperature, (*b*) pH, (*c*) conductivity, (*d*) salinity, and (*e*) dissolved oxygen (DO) measured in enclosures (diamonds) and ambient harbour water (triangles). Solid symbols with solid line denote measurements taken during the first experiment (n = 30 enclosures, n = 12 harbour); open symbols with broken line denote measurements taken for the second experiment (n = 24 enclosures, n = 12 harbour). Minor, but statistically significant, differences between enclosures and ambient water existed for conductivity and salinity (both experiments) and dissolved oxygen (experiment one only).



ment. Analysis of the best fit trajectory for estimates of establishment probability, $P(E_{best,\ low})$ and $P(E_{best,\ high})$, for enclosure populations indicate that all six study species would be unable to produce persistent populations given the low inoculum densities proposed by the IMO (see Appendix A, Table A1). Given the wide CIs for the probability of establishment provided by the parametric bootstrap, however, and following a precautionary approach, we also report the upper projection trajectory at low $P(E_{upper,\ low})$ and high $P(E_{upper,\ high})$ values of C. Among the enclosure populations, *D. retrocurva*, *B. coregoni*, and *Bosmina* spp. exhibited moderate–high (0.56–0.86) probabilities of establishment at inoculum densities as high as 10% of C, while *Chydorus sphaericus*, *Ceriodaphnia lacustris*, and *D. galeata* exhibited negligible

Fig. 4. Relationship between inoculum density and probability of establishment after 100 days ($P(E_{appx})$) for high (open symbols) and low (solid symbols) critical reproductive threshold densities in natural (circles) and enclosure (triangles) populations of (*a*) *Bosmina* spp., (*b*) *Daphnia retrocurva*, (*c*) *Chydorus sphaericus*, (*d*) *Bosmina coregoni*, (*e*) *Ceriodaphnia lacustris*, and (*f*) *Daphnia galeata mendotae*. Note *x* axes are scaled to a maximum of 0.1*C*, for each species.

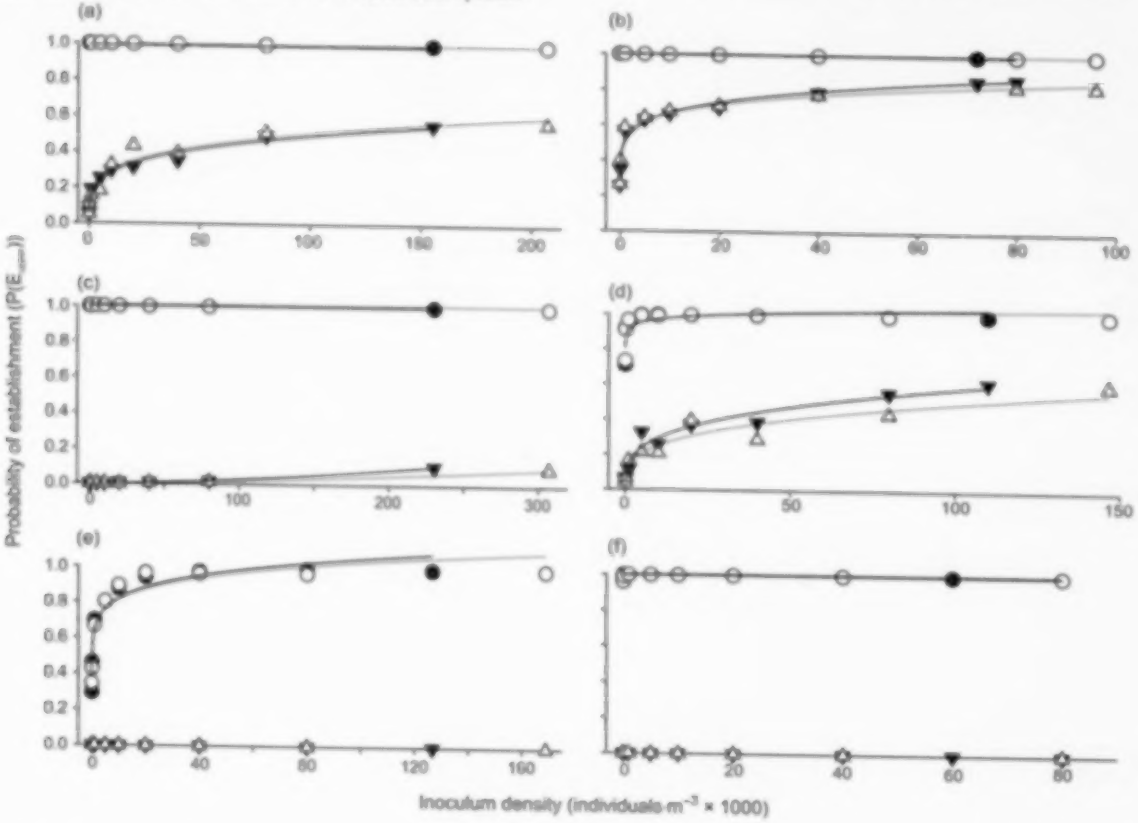
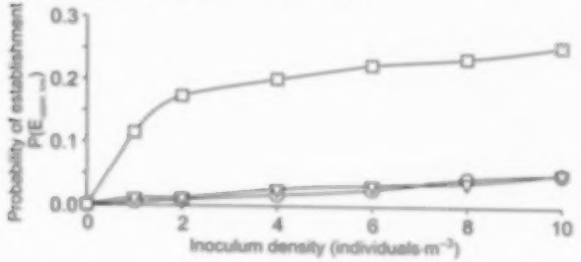


Fig. 5. Predicted probabilities of establishment ($P(E_{appx,\ 1000})$) for *Bosmina* spp. (circles), *Bosmina coregoni* (triangles), and *Daphnia retrocurva* (squares) in enclosures given inoculum densities of 1–10 individuals·m^{-3}. Establishment probabilities for the remaining three species were 0 at these inoculum densities.

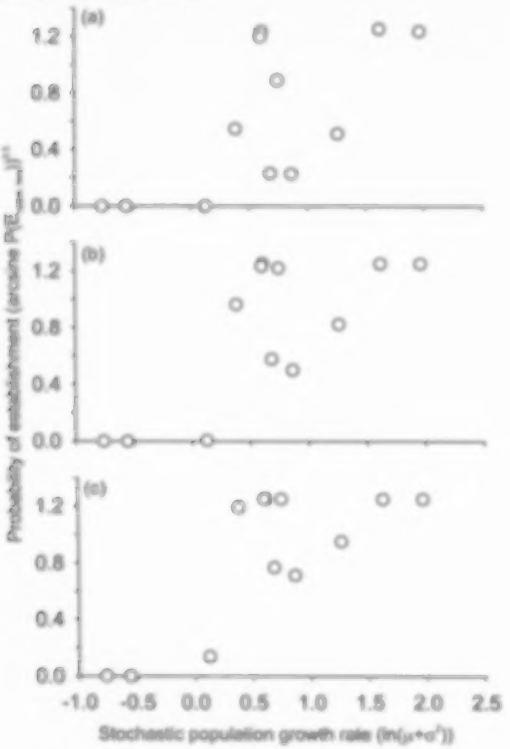


probabilities of establishment (Fig. 4). Only *D. retrocurva* exhibited a low–moderate (0.25–0.27) probability of establishment at inoculum densities of 10 individuals·m^{-3} (Fig. 5). *Bosmina coregoni* and *Bosmina* spp. exhibited very low probabilities of establishment (0.04–0.05) at this inoculum density, while the remaining species appear incapable of establishment given such low inocula.

The probability of establishment increased with stochastic population growth rate, supporting our initial hypothesis and indicating that these results can be interpreted for a broader array of taxa than directly measured in this study (Fig. 6). Changes in initial densities, as defined by *d*, increase both the regression coefficient and the coefficient of determination of the linear regression between stochastic growth rate and the probability of establishment. Separation of stochastic population growth rates into separate μ and σ^2 components reveal the strong influence exerted by high values of σ^2 (see Fig. 7). When σ^2 values are close to zero, probabilities of establishment are low, even for populations with high μ values. In addition, higher σ^2 values are correlated with higher probabilities of establishment, even for populations with low μ. This finding explains why some taxa with lower μ values (e.g., *B. coregoni*; μ = 0.302) had higher establishment probabilities than taxa with higher μ values (e.g., *D. galeata*; μ = 0.331).

Using low or high levels of critical reproductive threshold densities had little effect on the probabilities of establishment for both natural and enclosure populations. Examining establishment probabilities at densities below the 10 individuals·m^{-3} benchmark (Fig. 5) indicates that the probability of

Fig. 6. Relationship between probability of establishment and stochastic population growth rate at three levels of initial density (log inoculum density, $d = \log C - \log D_0$): (*a*) $d = 12$, (*b*) $d = 6$, and (*c*) $d = 3$. The upper bound of the 95% confidence interval for σ^2 was used in the computations as an index of the maximum variance value under uncertainty.

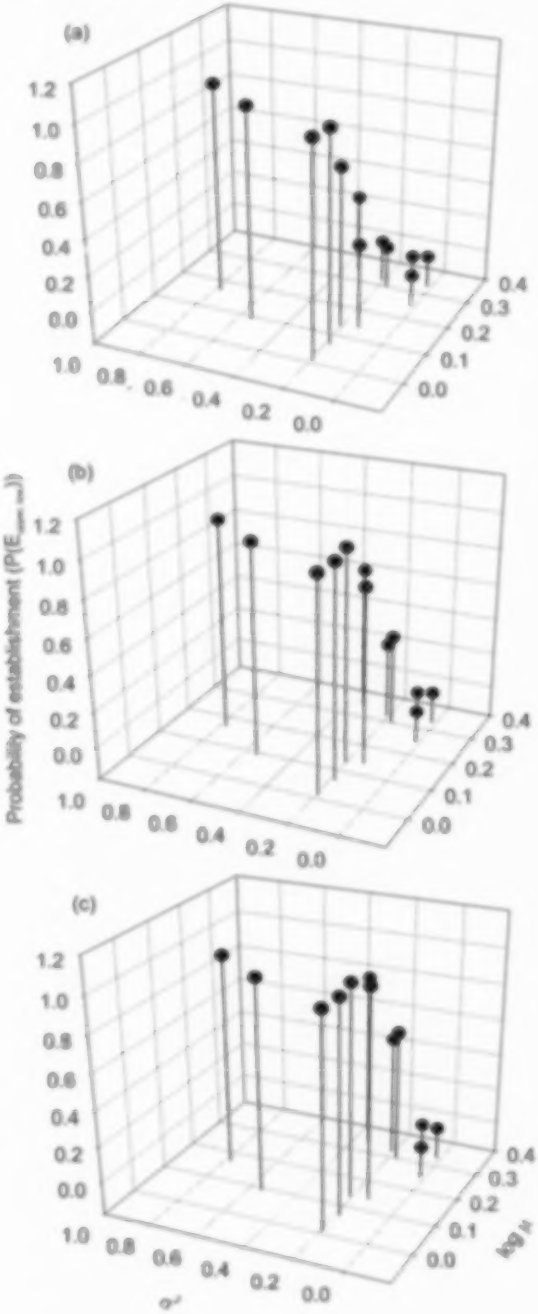


establishment can be greater than 0.1 for *D. retrocurva* at an inoculum density of only 1 individual·m^{-3}. Comparison with densities reported in the literature for ballast water following exchange (~100 individual·m^{-3}; Minton et al. 2005) indicate that compliance with the proposed IMO discharge standard could result in a threefold reduction in the probability of establishment for some species. It should be noted, however, that ballast water exchange is estimated to be equally effective for half of the species studied.

Discussion

We used a novel methodology to estimate establishment probabilities of parthenogenetic taxa as the probability of reaching critical reproductive threshold densities. Because of the large variation in stochastic population growth rates, the CIs surrounding the probabilities of establishment for Cladocera at 100 days in the future were large, realistically reflecting uncertainty due to observed variation and demographic stochasticity inherent in the experimental population growth rate data. This wide range of uncertainty is an important feature of invasion processes wherein propagules are continuously introduced to new environments without becoming established (see Carlton 1996). Complex interactions among propagule pressure, abiotic environmental conditions

Fig. 7. Probability of establishment ($P(E_{upper, time})$) as a function of mean log population growth rate (μ) and variance (σ^2) at (*a*) $d = 12$, (*b*) $d = 6$, and (*c*) $d = 3$ for data collected from enclosure and natural populations. Values of d (log inoculum density, $d = \log C - \log D_0$) are generated with initial densities ranging from 7–10, 1000–5000, and 40 000–80 000 individuals·m^{-3} for $d = 12$, $d = 6$, and $d = 3$, respectively.



(MacIsaac et al. 2001), and density-dependent effects (Shigesada and Kawasaki 1997) may act together to reduce establishment probabilities, thus requiring multiple introduction events for a successful invasion (Lockwood et al. 2005). While our best fit estimates of establishment probabilities for inocula less than 10 individuals·m^{-3} are nil, indicating that the proposed ballast water discharge standards will be very effective for even parthenogenetic taxa, we can not disregard the higher probabilities of establishment portrayed by the upper projection trajectories that may include rare invasion events.

The higher variance in population growth rates observed for natural populations is most likely driven by the prevalence of patchy population structure, which is reduced inside enclosures because of physical limitations and decreased effects of biotic and abiotic drivers of plankton patchiness (see discussion of patchiness below). In addition, the short time-series data may have led to increased variance, possibly leading to inflated probabilities of establishment. Increasing the number of sampling intervals might increase the accuracy of the diffusion approximation (Dennis et al. 1991). Morris and Doak (2002) suggest that 10 time points should be the minimum requirement to apply the diffusion approximation; however, the estimation of establishment probabilities close to 1 for Cladocera from natural populations in the harbour indicates that shorter time-series data (e.g., five intervals) can be useful. Longer time-series data could be obtained by extending the duration of enclosure experiments, but this might result in artificial population trajectories (see Bloesch et al. 1988). Alternatively, longer time-series data could be obtained by decreasing the sampling interval. This approach is also problematic, however, as approximately 5% of the enclosure population was withdrawn with each sample, and more frequent sample collection might undermine the ability of enclosed populations to reach maximum population growth rates.

The mean log population growth rates measured from the enclosure experiments are similar to those obtained from life-table and demographic experiments for other Cladocera (e.g., Goulden et al. 1982; Nandini and Sarma 2000, 2003). At first glance, the inferred critical reproductive threshold densities appear high, being one to four orders of magnitude greater than natural population densities measured here; however, these observed densities do not represent population maxima recorded throughout the season in previous years and at different depths (O.E. Johannsson and K.L. Bowen, unpublished data). Furthermore, our estimates for *Ceriodaphnia lacustris* ($1.3 \times 10^6 - 1.7 \times 10^6$ individuals·m^{-3}) were slightly lower than those experimentally derived for *Ceriodaphnia* cf. *dubia* Richard ($2 \times 10^6 - 3 \times 10^6$ individuals·m^{-3}) by Rose et al. (2002). At any rate, substantial change (25%) to the absolute value of critical reproductive threshold densities in our model has little influence on the resulting projections.

Limitations of the analysis

Our approach to assessing the probability of establishment is limited and constitutes a first step towards a more comprehensive methodology incorporating additional complexities intrinsic to the establishment of nonindigenous species. We have taken a precautionary approach by deliberately investigating establishment success under favourable physical, chemical, and biological conditions (e.g., reduced competition and predation inside enclosures). As many taxa introduced via ballast water are actually introduced to locations with suboptimal environmental conditions, our establishment probabilities are very precautionary. Additional factors affecting establishment success that are not included in our estimates include the timing of introduction (seasonality), the inoculation rate (effects of multiple introduction events), and total inoculum size (irrespective of density), each of which are discussed below.

The first factor, time of introduction, could be addressed by running several mesocosm experiments spread over the entire growing season. Alternatively, predictive equations of stochastic population growth as a function of Julian date (e.g., Drake et al. 2006) or temperature (e.g., Savage et al. 2004) could be used to analyze establishment probabilities for different times of year. Seasonal constraints on adult survival emphasize the importance of the timing of introduction; the later an introduction event occurs in the growing season, the greater the propagule pressure required to reach the critical reproductive threshold density for population establishment before environmental conditions deteriorate (e.g., Drake 2004).

The second factor, inoculation rate, could be addressed with information about site-specific number and frequency of inocula and a spatially explicit model simultaneously simulating population growth and spread, such as the reaction–diffusion model used by Lewis and Kareiva (1993). Population demographics (i.e., propagule pressure theory) predict that the probability of establishment will increase with the number of propagules released and the frequency of introduction events (Allendorf and Lundquist 2003; Lockwood et al. 2005), particularly under low dispersion rates (Drake et al. 2005). One could argue that our estimates of establishment probability should account for the scenario in which ballast water is being discharged in the same physical location multiple times during the spring and summer growth season. In contrast, we suggest that high dispersal rates in both time and space, particularly for zooplankton introductions, might nullify the argument that inoculation rate functions as cumulative increments in density. Rather, multiple inoculation events would serve to increase the probability of establishment by increasing the chance that propagules will be introduced to a new location during optimum environmental conditions, maximizing the probability of reaching critical reproductive threshold densities. Unless ballast discharge events happen extremely close in both time and space, active and passive dispersal of zooplankton would make encounter probabilities extremely small.

Similarly, total inoculum size (i.e., volume of ballast water discharged) is not factored into our predictions, wherein large inocula could serve to move establishment probabilities towards upper trajectories by increasing the likelihood that propagules would encounter favourable conditions at a microhabitat scale. Furthermore, biological (e.g., active swarming) or physical (e.g., passive aggregation due to water hydrodynamics or wind) factors after introduction may increase establishment probabilities if large numbers of propagules accumulate in one location. It has been previously demonstrated that biological and physical factors can

result in zooplankton patches with densities three orders of magnitude greater than median densities in the surrounding area (George and Edwards 1976; Folt and Burns 1999), although the frequency at which this occurs is unknown. Our estimates of establishment probability inherently assume that inoculation densities are uniformly distributed and may underestimate establishment probabilities in habitats with high zooplankton patchiness. We suggest that the aggregation of zooplankton might play an extremely important role in the invasion process and that future predictions of invasion success should incorporate drivers of zooplankton patchiness.

Finally, it must be acknowledged that we address a single limit in the discharge standard and that additional studies are needed to evaluate the efficacy of the limits for other taxa (e.g., phytoplankton, bacteria, and pathogens). Our estimates for parthenogenetic zooplankton are based on only six species in a favourable habitat and may overestimate the average risk posed by zooplankton; however, the risk posed by some taxa may be underestimated. Parthenogenetic Rotifera with extremely rapid population growth rates may pose a high risk of introduction. As an example, we noted during these experiments that populations of *Asplanchna* spp. grew from founding sizes less than 10 individuals·m^{-3} to large populations producing diapausing eggs in less than 2 weeks. It has been suggested that rotifers pose a risk of invasion via ballast water and sediments, with several new species documented (but perhaps not established) in the Great Lakes region (Bailey et al. 2005; Gray et al. 2005); the potential impact of nonindigenous rotifers is unknown.

Efficacy of the proposed ballast water discharge standard

Studies of community composition of ballast water indicate that parthenogenetic taxa are encountered both infrequently and at low density (Harvey et al. 1999; Duggan et al. 2005; Drake and Lodge 2007). The propensity for rapid population growth and history of invasion success in the Great Lakes by these taxa, however, warrants a close evaluation of the efficacy of the proposed ballast water standards for parthenogens. Our results indicate that the proposed regulation for zooplankton load in ballast water will be very effective, but that stochastic invasion events will remain possible. Assuming that ballast water discharge is composed of 10 individuals·m^{-3} of a single parthenogenetic species, low–moderate probabilities of establishment may result, particularly if propagules are introduced no later than 40 days before the onset of environmental conditions detrimental for survival.

Ballast water exchange, the current status quo for ballast water management, does not appear capable of meeting the discharge limits set by the IMO (Minton et al. 2005; Gray et al. 2007). Our model indicates that any ballast water treatment technologies meeting the proposed standards could reduce the probability of establishment for some parthenogenetic species threefold, although ballast water exchange is estimated to be equally effective for half of the species studied. We must caution, however, that the proposed discharge standards are based entirely on propagule load and no longer incorporate any measure of environmental mismatching into ballast water management. As such, a ship that uses treatment technology to meet the discharge standards after taking ballast at a freshwater port could effectively pose the same risk (to a freshwater recipient port) as a ship having exchanged ballast water from the same port; although the exchanged ballast water is expected to have a higher total propagule load, both ships could theoretically carry the same density of high risk (i.e., freshwater) propagules (<10 individuals·m^{-3}; see Gray et al. 2007). We suggest that management of ballast water carried between freshwater ports could be most effectively managed by requiring ships to conduct ballast water exchange prior to treatment with technology to ensure that the 10 individuals·m^{-3} discharged are almost entirely marine, low-risk species. This appears to be the best protection that can be provided under current operational conditions.

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Appendix A

Table A1 appears on the following pages.

Table A1. Numerical probabilities of establishment estimated using a stochastic diffusion approximation for six Cladocera at inoculum densities ranging from 10 individuals·m^{-3} to 10% of the species-specific critical reproductive threshold density ($0.1C_i$).

		Probability of establishment					
Species	Inoculum density (individuals·m^{-3})	$P(E_{lower,\ low})$	$P(E_{best,\ low})$	$P(E_{upper,\ low})$	$P(E_{lower,\ high})$	$P(E_{best,\ high})$	$P(E_{upper,\ high})$
Bosmina coregoni	10	0	0	0.05	0	0	0.04
	100	0	0	0.07	0	0	0.07
	1 000	0	0	0.11	0	0	0.17
	5 000	0	0	0.33	0	0	0.21
	10 000	0	0	0.26	0	0	0.21
	20 000	0	7.0×10^{-7}	0.37	0	2.0×10^{-7}	0.40
	40 000	0	8.1×10^{-6}	0.39	0	2.9×10^{-6}	0.29
	80 000	0	9.4×10^{-5}	0.56	0	3.4×10^{-5}	0.44
	$0.1C_i$	0	2.9×10^{-4}	0.62	0	2.9×10^{-4}	0.60
Bosmina spp.	10	0	0	0.05	0	0	0.05
	100	0	0	0.09	0	0	0.10
	1 000	0	0	0.19	0	0	0.16
	5 000	0	0	0.25	0	0	0.18
	10 000	0	0	0.30	0	0	0.33
	20 000	0	$1.7\text{x }10^{-6}$	0.32	0	0	0.43
	40 000	0	1.4×10^{-5}	0.35	0	6.0×10^{-6}	0.39
	80 000	0	1.2×10^{-4}	0.49	0	4.9×10^{-5}	0.51
	$0.1C_i$	0	9.0×10^{-4}	0.56	0	9.0×10^{-4}	0.57
Ceriodaphnia lacustris	10	0	0	0	0	0	0
	100	0	0	0	0	0	0
	1 000	0	0	0	0	0	0
	5 000	0	0	0	0	0	0
	10 000	0	0	0	0	0	0
	20 000	0	0	0	0	0	0
	40 000	0	0	0	0	0	0
	80 000	0	0	2.0×10^{-6}	0	0	0
	$0.1C_i$	0	0	7.8×10^{-6}	0	0	0
Chydorus sphaericus	10	0	0	0	0	0	0
	100	0	0	0	0	0	0
	1 000	0	0	2.0×10^{-5}	0	0	$3.2\text{ x}10^{-4}$
	5 000	0	0	4.4×10^{-5}	0	0	7.5×10^{-4}
	10 000	0	0	7.9×10^{-4}	0	0	5.7×10^{-4}
	20 000	0	0	6.9×10^{-3}	0	0	2.9×10^{-4}
	40 000	0	0	9.2×10^{-3}	0	0	5.7×10^{-3}
	80 000	0	0	0.02	0	0	0.01
	$0.1C_i$	0	0	0.11	0	0	0.10

Table A1 (*concluded*).

Species	Inoculum density (individuals·m^{-3})	Probability of establishment					
		$P(E_{lower,\ low})$	$P(E_{best,\ low})$	$P(E_{upper,\ low})$	$P(E_{lower,\ high})$	$P(E_{best,\ high})$	$P(E_{upper,\ high})$
Daphnia galeata mendotae	10	0	0	0	0	0	0
	100	0	0	0	0	0	0
	1 000	0	0	0	0	0	0
	5 000	0	0	0	0	0	0
	10 000	0	0	0	0	0	0
	20 000	0	0	0	0	0	0
	40 000	0	0	0	0	0	0
	80 000	0	0	0	0	0	0
	$0.1C_i$	0	0	0	0	0	0
Daphnia retrocurva	10	0	0	0.26	0	0	0.27
	100	0	0	0.35	0	0	0.40
	1 000	0	2.0×10^{-6}	0.57	0	0	0.59
	5 000	0	4.2×10^{-5}	0.63	0	2.4×10^{-5}	0.64
	10 000	0	1.7×10^{-4}	0.67	0	1.0×10^{-4}	0.68
	20 000	0	7.0×10^{-4}	0.70	0	3.9×10^{-4}	0.71
	40 000	0	2.9×10^{-3}	0.79	0	1.6×10^{-3}	0.78
	80 000	0	0.01	0.87	0	6.5×10^{-3}	0.83
	$0.1C_i$	0	9.4×10^{-3}	0.86	0	6.5×10^{-3}	0.83

Note: Estimates are given for the probability of establishment at 100 days into the future, using low and high estimates of critical reproductive threshold density and using data measured from enclosure populations.

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Effects of sampling effort, assemblage similarity, and habitat heterogeneity on estimates of species richness and relative abundance of stream fishes

Jesse R. Fischer and Craig P. Paukert

Abstract: We estimated the sampling effort required to accurately estimate species richness and to detect changes in catch-per-unit-effort (CPUE) in four Great Plains, USA, streams. The number of sampled reaches (i.e., <1 km) required to estimate stream-segment (i.e., 20–28 km) species richness decreased with increased sampled reach length (i.e., 10, 20, 40, or 60 mean stream widths, MSW), whereas total sampling effort decreased with a greater number of shorter sampled reaches. Collecting all species in a stream segment required all sampled reaches (i.e., 10) of a length equal to 40 or 60 MSW. The number of stream reaches sampled with lengths equal to 40 MSW required to detect a 50% change in CPUE of common species (i.e., total abundance > 1% of total catch) with $\beta = 0.80$ ranged from 7 to 630 (mean = 99) and decreased with longer sampled reaches. A greater number of sampled reaches were needed to detect 90% of species richness and 25% changes in CPUE when Jaccard's similarity of samples of stream fish assemblages and habitat heterogeneity was lower within streams. Our results suggest that homogeneous stream segments require more sampled reaches to characterize fish assemblages and monitor trends in fish abundance.

Résumé : Nous avons estimé l'effort d'échantillonnage requis pour évaluer correctement la richesse spécifique et pour détecter les changements dans les prises par unité d'effort (CPUE) dans quatre cours d'eau de la région des Grandes Plaines, É.-U. Le nombre de sections échantillonnées (de <1 km) nécessaires pour estimer la richesse spécifique dans un segment (soit 20–28 km) de cours d'eau diminue en fonction de l'augmentation de la longueur des sections échantillonnées (largeurs moyennes des cours d'eau (MSW) de 10, 20, 40 ou 60 m), alors que l'effort total d'échantillonnage diminue avec l'augmentation du nombre de sections plus courtes échantillonnées. La récolte de toutes les espèces dans un segment de cours d'eau nécessite que toutes les sections échantillonnées (soit 10) soient d'une longueur égale à 40 ou 60 MSW. Le nombre de sections de cours d'eau de longueur égale à 40 MSW requis pour détecter un changement de 50 % de CPUE des espèces communes (avec une abondance totale > 1% des captures totales) avec $\beta = 0{,}80$ varie de 7 à 630 (moyenne = 99) et décroît si les sections échantillonnées sont plus longues. Il faut échantillonner un plus grand nombre de sections afin de détecter 90 % de la richesse spécifique et des changements de 25 % de CPUE lorsque la similarité de Jaccard est plus faible dans les échantillons des peuplements de poissons et que l'hétérogénéité des habitats est réduite dans les cours d'eau. Nos résultats indiquent que, dans les segments homogènes de cours d'eau, il faut échantillonner un plus grand nombre de sections afin de caractériser les peuplements de poissons et de suivre les tendances d'abondance des poissons.

[Traduit par la Rédaction]

Introduction

Stream fish assemblages are often sampled at a few locations to describe species richness and catch-per-unit-effort (CPUE) of individual species across a larger spatial scale. These data are then used to develop management and conservation decisions (e.g., conservation of areas of greatest diversity), evaluate ecosystem health (e.g., index of biotic integrity) (Karr 1981; Fausch et al. 1990), describe fish distributions (Rahel and Hubert 1991), and understand patterns of fish assemblage structuring within streams (Angermeier and Winston 1999). The accuracy and quality of fish assemblage data are therefore critical to the validity of these decisions.

Fausch et al. (2002) proposed that the fundamental problem with the current conservation and management of stream fish is the lack of scientific research relevant over large spatial and temporal scales and argued that the current spatial gap of knowledge exists between reaches (i.e., <1 km) and segments (i.e., 1–100 km). Understanding

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relations between environmental and fish assemblage characteristics is often explored using one assemblage sample from a reach to characterize a segment (Gido et al. 2006) or entire catchment (Smith and Kraft 2005; Diana et al. 2006; Heitke et al. 2006). This increases the need for accurate estimates of assemblage attributes and to understand the sampling effort required to characterize streams segments. It is therefore important to understand the relationship between fish assemblage data collected at reach scales and that of entire stream segments.

Ideally, discrete samples of fish assemblages are representative of fish assemblages at larger spatial scales. However, it is often impossible to sample all species of a community (Krebs 1998), which creates difficulties in determining the amount of sampling effort required to describe an assemblage at a larger spatial scale. Second, the number of species collected increases as stream area or sample length and the number of samples increases (Angermeier and Schlosser 1989; Lyons 1992; Peterson and Rabeni 1995). Finally, species are not evenly distributed within the stream due to habitat heterogeneity (Gorman and Karr 1978; Angermeier and Smogor 1995), and variability in spatial distributions of rare species (Lyons 1992; Paller 1995) affects species detection. Therefore, the relationship of fish assemblages within a reach to those at greater spatial scales (e.g., segments, entire streams, catchments) is not well understood.

Many studies have attempted to determine the sampling effort or sampled length, based on mean stream width (MSW), required in wadeable streams reaches to collect a high percentage (i.e., 90%–100%) of the species present (Angermeier and Smogor 1995; Dauwalter and Pert 2003; Reynolds et al. 2003). Lyons (1992) found that the length of sampled reaches required to obtain asymptotic species richness ranged from 32 to 104 MSWs (mean = 29) in Wisconsin streams, whereas Paller (1995) determined sampled reach lengths of 35–158 MSWs (mean = 87) were required in South Carolina coastal plain streams. Therefore, the sampling effort required to obtain asymptotic species richness in streams may vary among regions and (or) stream size. However, the need to develop standardized methods for sampling fish assemblages has resulted in established protocols that recommend a sampling length of 40 MSW (Peck et al. 2006). These programs are often focused on determining conditions and monitoring trends over time, so fish assemblage sampling is typically conducted at a single reach (Moulton et al. 2002). It is therefore necessary to evaluate the natural variability in fish assemblage characteristics with multiple reaches sampled within stream segments using these standardized methods.

Most studies of sampling effort do not extensively sample multiple reaches at each stream. However, Matthews (1990) found that increasing the number of sampling sites better represented the fish assemblage in a Virginia, USA, river. Smith and Jones (2005) determined that first- to third-order streams of Great Lakes watersheds required 76–115 sampled reaches of lengths equal to 30 MSWs to collect 100% of estimated species richness. Additionally, Peterson and Rabeni (1995) determined that at least 24 sampled channel classification units (i.e., scour, slackwater, transition, and riffle) that ranged in size from 33 to 660 m^2 were needed to obtain species richness with a 10% level of precision in Missouri streams and that spatial variation exceeded temporal variation. This suggests that more samples may be needed to accurately describe the fish assemblage structure in many streams because of habitat heterogeneity. For rare fishes, high variation in catch rates leads to low precision and thus an unobtainable number of samples needed to detect trends (Paukert 2004). Even monitoring trends in common species may require more sampling than is feasible (Quist et al. 2006). Therefore the evaluation of the effort needed in wadeable streams to describe assemblage structure and monitor fish populations is important to both local and regional ecosystem management.

Our objectives were to determine the sampling effort needed to describe fish assemblages in four midsized (i.e., 10–29 m mean width), wadeable Great Plains streams across large spatial extents (i.e., 20–28 km stream segments) and to attempt to relate differences in sampling effort required to estimate assemblage characteristic and habitat differences between streams. Specifically, we wanted to determine (*i*) the number and length of sampled reaches required to collect precise (75%, 90%, and 100%) estimates of all species and common species (i.e., comprising >1% of the cumulative catch for each stream) within stream segments and (*ii*) the number and length of sampled reaches required to detect 25%, 50%, and 75% changes in CPUE (with $\beta = 0.80$) of common fish species. Differences in the number and length of sampled reaches required to describe species richness estimates and changes in CPUE between streams were evaluated using (*i*) species–area relationships to determine differences in species accumulation rates, (*ii*) fish assemblage similarity among sampled reaches to determine the effect of fish assemblage structure, and (*iii*) physical habitat data. Our findings increase the understanding of the relationship of fish assemblage data collected at individual reaches to those at larger spatial scales in midsized wadeable streams with varying species distributions, assemblage structure, and habitat structure. We provide researchers with a reference for the appropriate sampling effort needed to improve the development of wadeable stream protocols when estimating species richness and monitoring fish CPUE at large spatial scales (i.e., stream segments).

Materials and methods

Site description

Four streams in Nebraska and Kansas, USA, were sampled from 15 May to 30 June 2006, with individual streams sampled in five days or less to minimize temporal variation among samples within streams. Streams were selected to represent stream characteristics found in the Great Plains and were located in three of the 12 major basins (i.e., Kansas, Niobrara, and Platte) of the Missouri River. Streams were also selected on the basis of access so that intensive longitudinal sampling (i.e., 20–28 km) could be conducted in a localized area to determine species presence for the stream segment. The Niobrara River, a National Scenic River, is located in north-central Nebraska and is a tributary to the Missouri River. Blue Creek is located in western Nebraska and is a tributary to the North Platte River. The North Loup River is a tributary to the Loup River that drains into the Platte River. The North Loup River is located in the

Table 1. Characteristics of 10 sampled reaches in each of four streams in Nebraska and Kansas sampled in the summer of 2006.

	Blue Creek	Niobrara River	North Loup River	West Branch Mill Creek
Species richness (*N*)	13	21	19	32
Stream-segment length (m)	28 416	20 125	25 232	25 719
Mean distance between sampled reaches (m)	3 157 (330)	2 236 (202)	2 804 (409)	2 858 (436)
Mean width (m)	9.94 (27.1)	28.89 (19.2)	10.95 (23.8)	11.39 (43.7)
Mean depth (m)	0.45 (13.4)	0.16 (26.7)	0.33 (17.4)	0.36 (69.6)
Filamentous algae (% cover)	6.39 (26.3)	2.15 (53.2)	0.54 (152.8)	21.54 (100.0)
Macrophytes (% cover)	30.59 (56.9)	0.59 (130.4)	13.06 (74.0)	0.00 (0.0)
Large woody debris (% cover)	0.00 (0.0)	0.03 (144.1)	0.00 (0.0)	0.33 (64.0)
Small woody debris (% cover)	0.28 (64.7)	0.08 (203.7)	0.00 (0.0)	0.32 (200.3)
Overhanging vegetation (% cover)	13.12 (76.3)	1.10 (48.6)	1.63 (46.3)	0.10 (122.5)
Undercut bank (% cover)	0.06 (185.4)	0.03 (39.8)	0.06 (100.3)	0.12 (81.6)
Boulder (% cover)	0.00 (0.0)	0.60 (82.0)	1.12 (128.8)	0.18 (124.1)

Note: Standard error of mean distance between sampled reaches and coefficient of variation of habitat variables is given in parentheses.

central Nebraska Sandhills region. The West Branch Mill Creek is located in the Flint Hills region of eastern Kansas and is a tributary to the Kansas River. A summary of the physical characteristics of each stream is provided (Table 1).

Data collection

Stream-segment estimates of fish assemblage characteristics were determined with 10 systematically sampled reaches with a minimum of 1 km between reaches (Fig. 1). Each sampled reach was at least 60 MSW or 1 km in total length. Sampled reaches were subdivided into sampling lengths of 10, 20, and 40 times the MSW. The four MSW sampled reaches were adjacent to each other (i.e., the 10 MSW reach was included in the 20 MSW reach, etc.). Fish were sampled using a towed, pulsed DC electrofisher with two anode poles. Electrofishing was conducted by two people with anodes and two netters in a single upstream run in a zigzag pattern with an emphasis to sample all available habitats (Lazorchak et al. 1998). Fish from each sampled reach were held in fish cages for identification after electrofishing for that entire sampled reach (i.e., 60 MSWs) was complete. Species were identified, counted, and released in the field. Unidentifiable and voucher specimens were preserved in 10% formalin and identified to species and counted in the laboratory.

Physical habitat was surveyed at six reaches on each stream using procedures adapted from the Environmental Protection Agency's (EPA) protocol for sampling wadeable streams (Peck et al. 2006) to determine the effect of habitat on sampling effort required to accurately estimate species richness. The only modification to these techniques was that individual sampling reaches were characterized with six transects (i.e., reduced from 11) with five sections between transects. Wetted width (m) was measured at each transect, and depth (m) was measured at three equally spaced points along the transect (i.e., one-quarter, one-half, and three-quarters of the wetted width distance) and divided by four to calculate transect mean depth (Arend 1999). Stream width and depth were calculated from the mean of transect depths and widths. Instream fish cover categories (filamentous algae, aquatic macrophytes, large woody debris, small woody debris, overhanging vegetation, undercut banks, and boulders) were estimated individually using five cover classes (absent, 0%; sparse, <10%; moderate, 10% to 40%; heavy, 40% to 75%; and very heavy, >75%) at each transect (Peck et al. 2006). The midpoint of each percentage

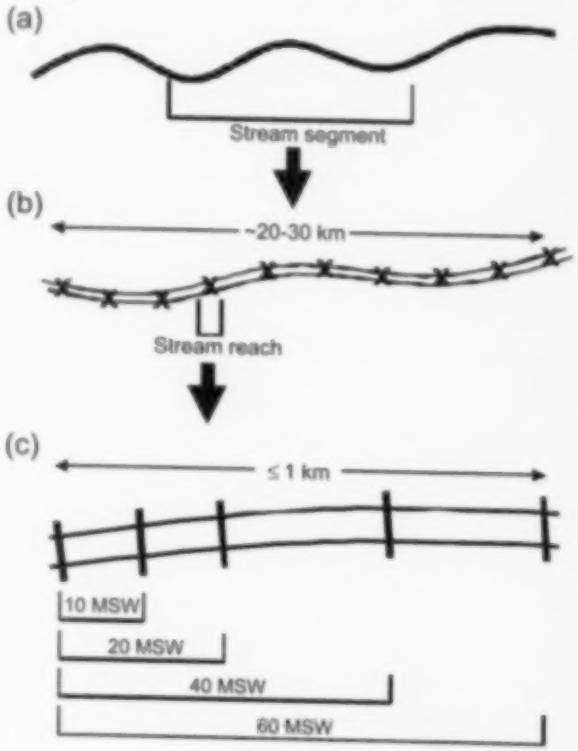


Fig. 1. (*a–b*) Stream segments of approximately 20–30 km were systematically sampled with 10 reaches and a minimum of 1 km between sampled reaches. (*c*) Sampled reaches were at least 60 times the mean wetted stream width (MSW) in length, with a maximum length of 1 km. Each sampled reach was subdivided into four sampling lengths (10, 20, 40, and 60 MSWs) for fish assemblage sampling.

class was used to calculate the mean percent cover for each reach. Coefficients of variation (CV) were calculated for each habitat parameter for each surveyed reach.

Sampling effort simulations

A Monte Carlo simulation that randomly selected sampled reaches (without replacement) from each stream was conducted to determine the number of sampled reaches needed to detect 75%, 90%, and 100% of all species collected in all samplings within each stream. The simulation methods used were similar to those explained by Quist et al. (2007). Total segment species richness was calculated as all species encountered with all 10 sampled reaches of length equal to 60 MSW or 1 km for each stream. The probability of sampling precise estimates of the total segment species richness was calculated by counting the number of 1000 simulations for each given number of sampled reaches in which species richness met or exceeded 75%, 90%, and 100% of the segment species richness (e.g., proportion of total segment richness with one sampled reach, two sampled reaches, three sampled reaches). The number of sampled reaches needed to detect 75%, 90%, and 100% of the collected species within a stream segment was determined when probability of detecting 75%, 90%, and 100% of segment richness exceeded 95%. Simulation results were plotted for each stream and sampled reach length (i.e., 10, 20, 40, and 60 MSW). All simulations were run using all species collected and then again for common species, defined as species comprising <1% of the cumulative catch for each stream (Paller 1995; Reynolds et al. 2003). Total sampling effort (i.e., cumulative number of MSWs or total sampling length for all sampled reaches) was determined for each combination of reach length and number of reaches required from simulation results (e.g., four sampled reaches of length equal to 20 MSW would equal a total sampling effort of 80 MSW).

Sample size estimation

The number of reaches needed to detect changes in CPUE (i.e., fish·100 m^{-1} of electrofishing) at various statistical power levels was determined using simple interactive statistical analysis (SISA; Uitenbroek 1997), which has been commonly used to determine needed sample sizes in fish studies (Allen et al. 1999; Tate et al. 2003; Paukert 2004). We estimated the number of reaches needed to detect 25%, 50%, and 75% changes in CPUE at four levels of statistical power (i.e., β = 0.60, 0.70, 0.80, and 0.90) for each species that accounted for greater than 1% of the cumulative catch for each stream. The mean number of sampled reaches needed for all common species was calculated for each stream and sampled reach length among all streams. An analysis of variance (ANOVA) was used to determine if the mean number of sampled reaches required to detect changes in CPUE of common species differed with a level of statistical power of β = 0.80 among streams and sampled reach lengths separately. A significance level of α = 0.05 was used for all sample size estimates. Comparisons among the number of required sampled reaches were conducted using pairwise comparisons with significance levels adjusted with a Bonferroni correction (α = 0.05/6 or α = 0.008).

Species–area relationship

The species–area relationship for each stream was calculated to determine if species accumulation variability among streams would provide insight into differences in the number of sampled reaches required for precise estimates of species richness and to detect changes in CPUE. The cumulative number of species collected and sampled area were $\log_{10}$ transformed and plotted for each stream and sampled reach length to determine the rate of species accumulation (z) (Ricklefs 2000). Linear regression was used to estimate the slope (z) across all sampled reach lengths for each stream. Statistical comparisons of species–area relationships were not conducted due to lack of independence of observations.

Fish assemblage structure

We evaluated the effect of longitudinal variation of sampled fish assemblages within streams on estimates of species richness among sampled reaches. Species presence or absence within sampled reaches was measured using Jaccard's similarity coefficient, a common metric of community similarity (Krebs 1998), and is useful in determining sampling sufficiency in stream fish assemblage surveys (Cao et al. 2001). Linear regression was used to describe the relationship between the mean Jaccard's similarity coefficient and the distance between sampled reaches to determine the overall fish assemblage variability for each stream. We also evaluated the ability of distance between sampled reaches to predict species similarity with a Mantel test (Mantel 1967). We compared distance matrices of Jaccard's similarity coefficients and distance between sampled reaches with a Mantel test to determine the statistical significances (α = 0.05) and strength of the association (Mantel 1967).

Habitat associations

The effect of instream habitat structure on differences in number of sampled reaches required for precise estimates of species richness and to detect changes in CPUE among streams were evaluated. First, a stepwise discriminant analysis was used to reduce the number of habitat variables and determine the subset of uncorrelated variables that best discriminated among streams (i.e., greatest amount of variation among measured habitat variables) from the set of nine habitat variable means and CVs (see earlier section Data collection). Next, a canonical discriminant analysis (CDA) was conducted with the new subset of significant habitat variables (Johnson 1998) to quantify the greatest amount of variability between streams. Linear regression was used to quantify the relationship between the number of sampled reaches with lengths equal to 40 MSW needed to collect 75%, 90%, and 100% estimates of the total and common species richness and the mean canonical axis scores for each stream.

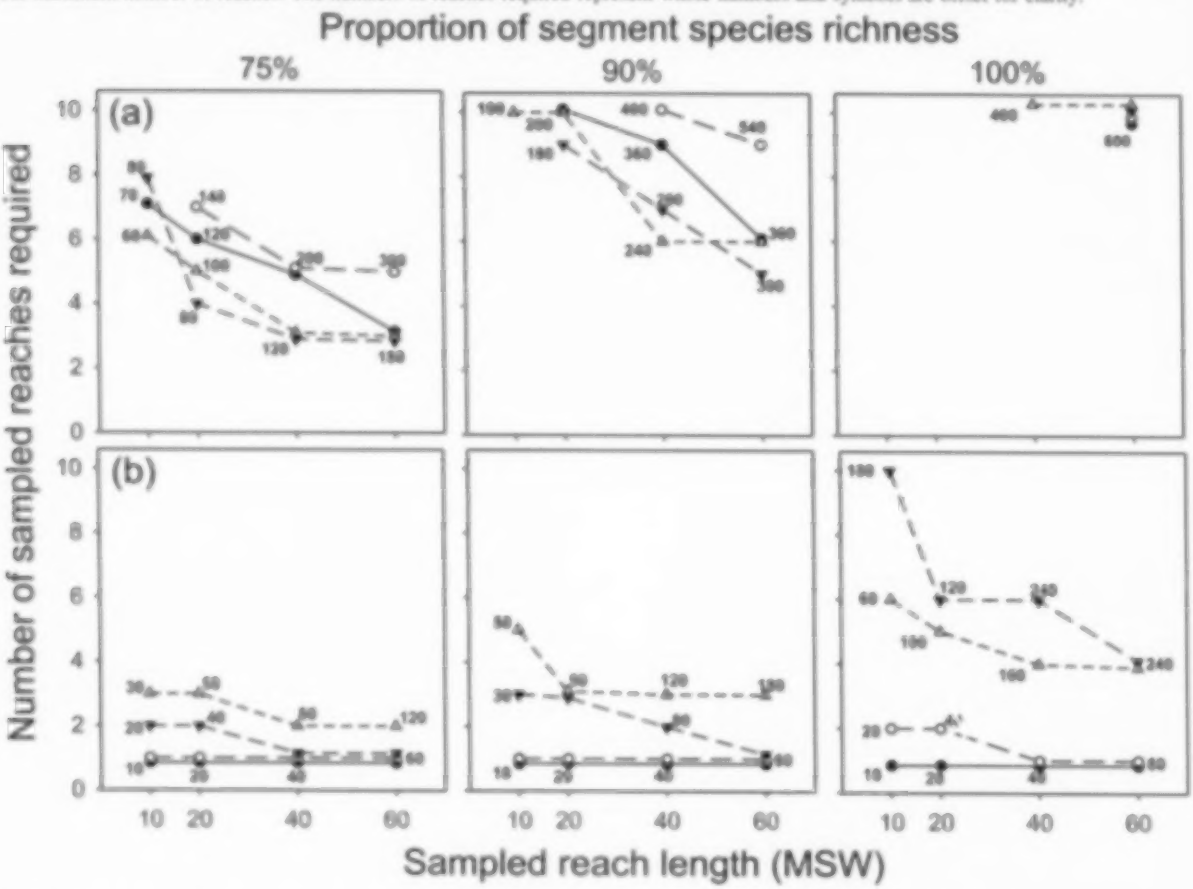
Results

Overall fish assemblage structure varied among streams. Total species richness ranged from 13 to 32 in the 20.1 to 28.4 km segments for the four streams sampled (Table 2). The number of fish sampled in each stream segment ranged from 2660 in Blue Creek to 27 894 in the Niobrara River (Table 2). Individual species CPUE ranged from 0 to 81.1 ($\bar{x}$ = 4.6) for Blue Creek, from 0 to 259.2 ($\bar{x}$ = 15.5) for the Niobrara River, 0 to 83.6 ($\bar{x}$ = 5.6) for the North Loup

Table 2. Percent abundance of fishes collected from four midsized streams of Nebraska and Kansas sampled using a towed electrofishing unit, summer 2006.

Scientific name	Common name	Blue Creek (N = 2660)	Niobrara River (N = 27 894)	North Loup River (N = 5273)	West Branch Mill Creek (N = 23 600)
Lepisosteus osseus	Longnose gar				0.068
Campostoma anomalum	Central stoneroller		0.183		36.78
Cyprinella lutrensis	Red shiner		11.325	3.717	6.475
Cyprinus carpio	Common carp		0.018	0.133	0.992
Hybognathus hankinsoni	Brassy minnow		0.09	5.385	
Luxilus cornutus	Common shiner				2.674
Lythrurus umbratilis	Redfin shiner				0.106
Notropis dorsalis	Bigmouth shiner	0.226	25.79	7.225	
Notropis rubellus	Rosyface shiner				9.737
Notropis stramineus	Sand shiner	0.414	47.58	15.172	1.479
Notropis topeka	Topeka shiner				0.017
Phenacobius mirabilis	Suckermouth minnow				6.869
Phoxinus eos	Northern redbelly dace			4.077	
Phoxinus erythrogaster	Southern redbelly dace				1.742
Pimephales notatus	Bluntnose minnow				11.051
Pimephales promelas	Fathead minnow	0.226	1.391	0.778	0.068
Pimephales vigilax	Bullhead minnow				0.034
Platygobio gracilis	Flathead chub			5.765	
Semotilus atromaculatus	Creek chub	72.782	2.416	2.333	1.326
Rhinichthys cataractae	Longnose dace	1.466	0.549	36.45	
Carpiodes carpio	River carpsucker			0.91	0.03
Catostomus commersonii	White sucker	10.301	6.586	9.71	4.742
Moxostoma erythrurum	Golden redhorse				1.114
Moxostoma macrolepidotum	Shorthead redhorse		3.09	1.346	
Ameiurus melas	Black bullhead			0.057	0.047
Ameiurus natalis	Yellow bullhead				0.225
Ictalurus punctatus	Channel catfish			0.114	
Pylodictis olivaris	Flathead catfish				0.14
Noturus exilis	Slender madtom				2.415
Noturus flavus	Stonecat	0.639	0.312	5.86	0.004
Esox lucius	Northern pike		0.007	0.019	
Oncorhynchus mykiss	Rainbow trout	0.038	0.004		
Salmo trutta	Brown trout	0.376			
Fundulus sciadicus	Plains topminnow	0.902	0.484		
Fundulus zebrinus	Plains killifish		0.004	0.645	
Culaea inconstans	Brook stickleback	0.301	0.004		
Ambloplites rupestris	Rock bass		0.054		
Lepomis cyanellus	Green sunfish	0.564		0.303	2.161
Lepomis humilis	Orangespotted sunfish				0.008
Lepomis macrochirus	Bluegill		0.004		0.318
Lepomis megalotis	Longear sunfish				3.106
Micropterus salmoides	Largemouth bass		0.004		0.288
Etheostoma nigrum	Johnny darter				0.585
Etheostoma spectabile	Orangethroat darter	11.767			5.174
Perca flavescens	Yellow perch		0.108		
Percina caprodes	Logperch				0.216
Percina maculata	Blackside darter				0.013

Fig. 2. Number of sampled reaches required to detect 75%, 90%, and 100% of segment species richness for four sampling lengths (i.e., 10, 20, 40, and 60 mean stream widths, MSW) of four wadeable streams in Nebraska and Kansas based on 1000 Monte Carlo simulations. Values are (*a*) for all species and (*b*) after the removal of rare species (i.e., species accounting for <1% of the cumulative catch for a stream). Symbols: Blue Creek, ●; Niobrara River, ○; North Loup River, ▼; West Branch Mill Creek, △. Total sampling effort (i.e., cumulative number of MSW) is indicated adjacent to symbols. Missing values indicate that the number of reaches required was greater than our maximum number of reaches. The numbers of reaches required represent whole numbers and symbols are offset for clarity.



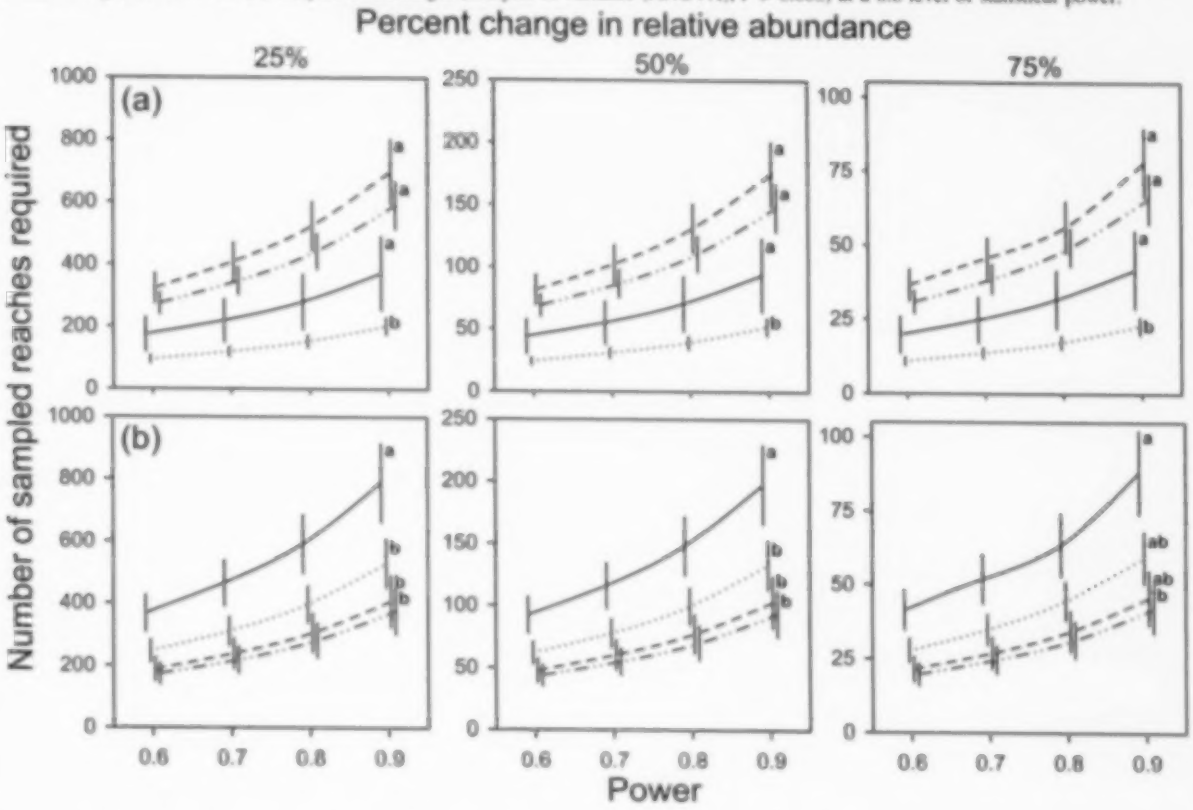
River, and 0 to 536.0 ($\bar{x}$ = 14.0) for the West Branch Mill Creek. The number of rare species ranged from eight in the North Loup River to 17 in West Branch Mill Creek. These species cumulatively represented 1.8% to 3.7% of the total fish collected for each stream. The proportion of rare species in the North Loup River (42.1%) and West Branch Mill Creek (53.1%) was less than that in the Niobrara River (66.7%) and Blue Creek (69.2%) (Table 2).

Habitat structure differed greatly between streams. Niobrara River was the shallowest (0.16 m) and widest (28.9 m) stream sampled with the least variability in width. Blue Creek was the narrowest (9.9 m) and deepest (0.45 m) stream with the least variability in depth, whereas North Loup River and West Branch Mill Creek were similar in mean width (11.0 and 11.4 m). West Branch Mill Creek exhibited the most variability in mean width and mean depth (Table 1). Mean percent cover of instream habitat variables and CVs varied considerably among streams (Table 1). For example, Niobrara River and West Branch Mill Creek had greater CVs for small woody debris, whereas Blue Creek and North Loup River had higher CVs for undercut banks.

Sample effort simulations

Total sampling effort to obtain 75% of the segment species richness was lowest with sampled reaches 10 MSW in length, which required six to eight sampled reaches and ranged from 60 to 80 MSWs of total sampling effort (Fig. 2*a*). However, 75% of all species were only obtained within three of the four streams with sampled reach lengths of 10 MSW (i.e., 75% of all species were not collected with all 10 sampled reaches in Niobrara River). Increasing reach length typically decreased the number of sampled reaches needed to collect 75% of the species. However, total effort either increased or remained constant with fewer sampled reaches of lengths greater than 10 MSW. For example, only three sampled reaches of 40 MSW were needed to collect 75% of all species in North Loup River, but this required a total effort of 120 MSWs (i.e., three sampled reaches of 40

Fig. 3. Mean number of sampled reaches required to detect a 25%, 50%, and 75% change in catch-per-unit-effort (i.e., fish·100 m^{-1}) of common fish species (i.e., after removal of rare species, <1% cumulative catch) for (*a*) four streams of Nebraska and Kansas and (*b*) four sampled reach lengths (mean stream width, MSW) at different levels of statistical power. In *a*, the solid line represents Blue Creek, the dotted line represents Niobrara River, the broken line represents North Loup River, and the dashed–dotted line represents West Branch Mill Creek. In *b*, the solid line represents 10 MSW, the dotted line represents 20 MSW, the broken line represents 40 MSW, and the dashed–dotted line represents 60 MSW. Bars represent one standard error. The mean number of sampled reaches needed with the same letter did not differ among (*a*) streams or (*b*) sampled reach length (analysis of variance (ANOVA), $P > 0.008$) at a 0.8 level of statistical power.



MSW). To achieve the same proportion of species richness, four sampled reaches with lengths of 20 MSW were needed (i.e., 80 MSWs of total sampling effort), which was equal to eight sampled reaches with lengths of 10 MSW (Fig. 2*a*). There was a greater amount of total sampling effort required to collect 90% of the species (i.e., 100–540 MSWs total sampling effort; Fig. 2*a*) in all streams, but total sampling effort was still lowest with a greater number of shorter sampled reaches. To estimate 100% of the segment species richness, all 10 sampled reaches with lengths of 60 MSWs were required for three streams (Fig. 2*a*), the maximum amount of sampling conducted in our study. All species were collected with 10 sampled reaches with lengths of 40 MSW for West Branch of Mill Creek. No combination of sampled reaches with lengths of 10 or 20 MSW collected 100% of the species (Fig. 2*a*).

The number of sampled reaches required to obtain similar estimates of common species (compared with that required for all species) decreased substantially for all streams (e.g., all common species were collected with just one sampled reach with a length of 10 MSW in Blue Creek) (Fig. 2*b*). The number of sampled reaches required to estimate 75% of the segment common species richness ranged from one to three sampled reaches with lengths of 10 MSW. Total sampling effort was less with sampled reaches of 10 MSW lengths for all streams (i.e., 10–30 MSWs of total sampling effort). One to five sampled reaches with lengths of 10 MSW were required to obtain 90% of the common species for all streams (Fig. 2*b*). Total sampling effort required to obtain 100% of common species ranged from 10 to 100 MSWs of total sampling effort between all streams and sampled reach lengths. Despite a greater number of sampled reaches, total sampling effort was minimized when sampled reach lengths were shorter (i.e., 10 MSWs). Overall, less effort was required to obtain common species than all species between all streams.

Sample size estimation

The mean number of sampled reaches required to detect 25%, 50%, and 75% changes in CPUE of common species ranged from 63 to 994, 17 to 249, and 8 to 111, respectively, among all levels of power for all streams (Fig. 3).

Fig. 4. Species–area relationships for four midsized streams in Nebraska and Kansas sampled in May–June 2006: (*a*) Blue Creek; (*b*) Niobrara River; (*c*) North Loup River; and (*d*) West Branch Mill Creek. Symbols represent length of sampled reaches for 10 (×), 20 (□), 40 (○), and 60 (△) mean stream widths. Lines represent linear regressions and *z* is the slope.

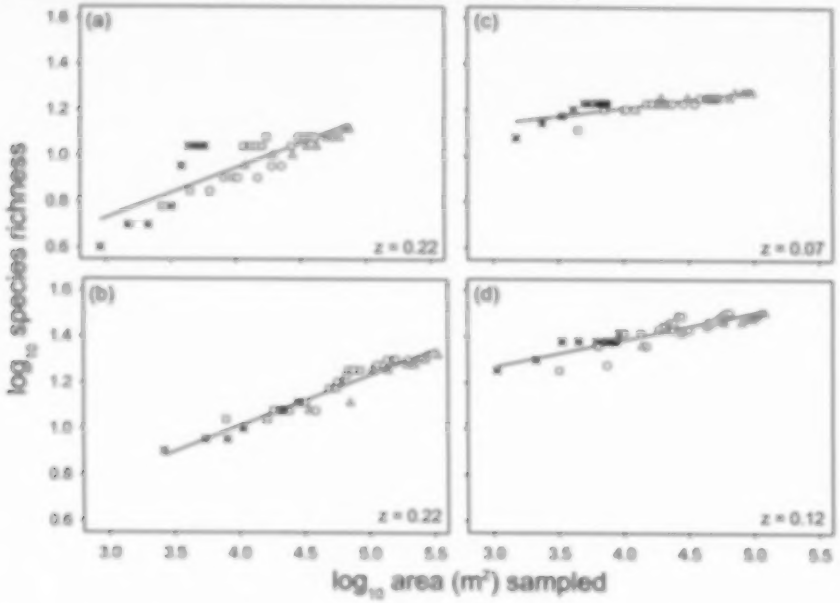
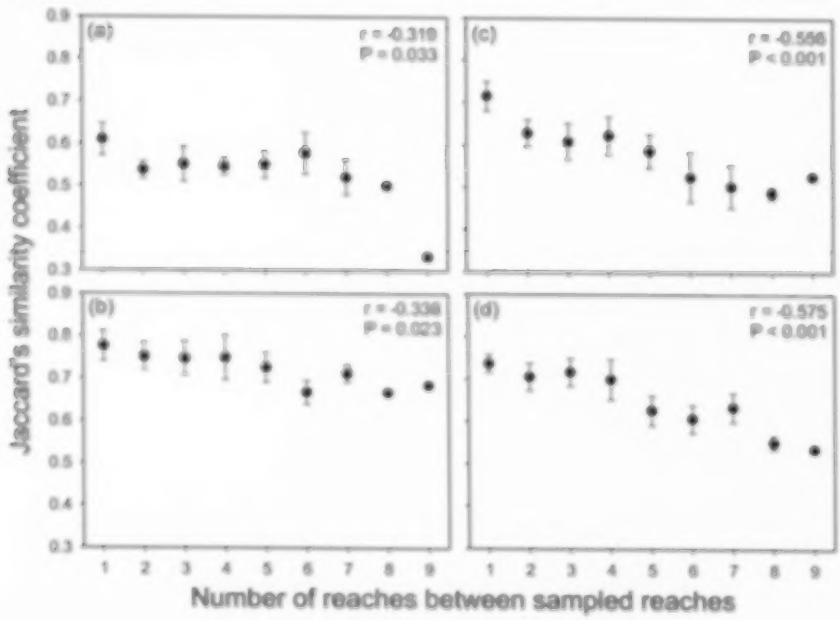
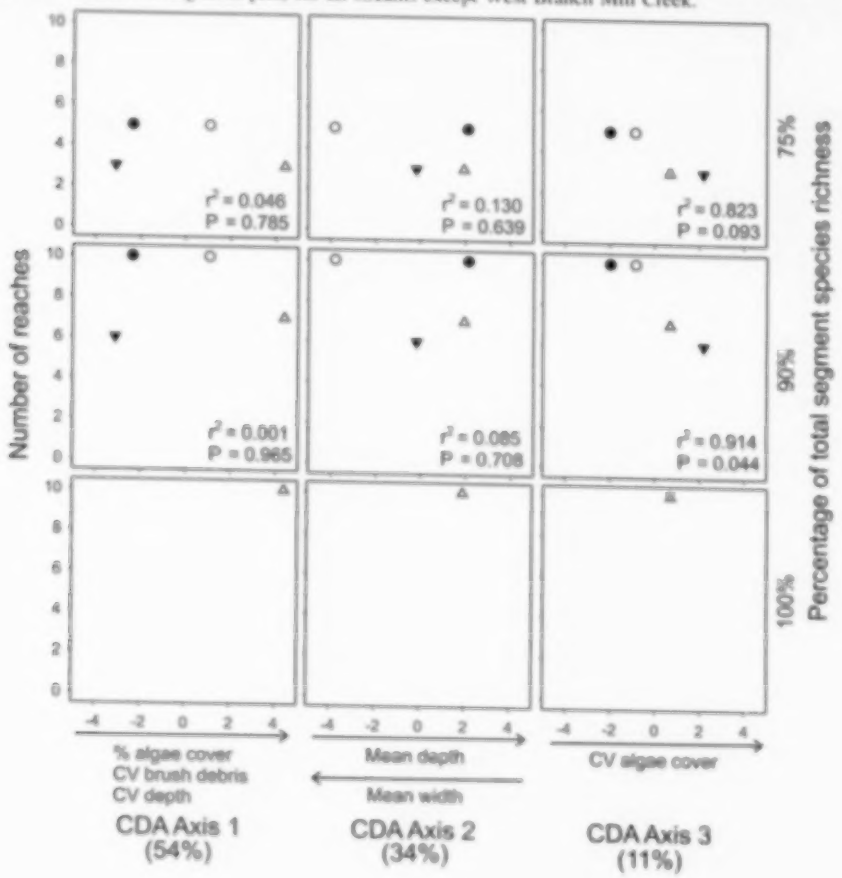


Fig. 5. Relationship between distance between samples (i.e., number of sampled reaches between selected 40 mean stream width reaches sampled) and mean Jaccard's similarity coefficients of sampled fish assemblages for four midsized streams in Nebraska and Kansas sampled with a pulsed DC, towed electrofisher: (*a*) Blue Creek; (*b*) Niobrara River; (*c*) North Loup River; and (*d*) West Branch Mill Creek. Error bars represent one standard error.



The number of sampled reaches needed varied among streams ($F_{[3,144]} = 5.20$, $P < 0.01$) and sampled reach lengths ($F_{[3,144]} = 4.10$, $P < 0.01$) for 25% changes in CPUE, among streams ($F_{[3,144]} = 5.07$, $P < 0.01$) and sampled reach lengths ($F_{[3,144]} = 4.10$, $P < 0.01$) for 50% changes in CPUE, and among streams ($F_{[3,144]} = 4.74$, $P < 0.01$) and sampled reach

Fig. 6. Relationship between the number of sampled reaches of lengths equal to 40 mean stream widths required to detect 75%, 90%, and 100% of segment species richness with a 95% probability and the mean canonical coefficients from the canonical discriminant analysis (CDA) of 24 habitat surveys from four midsized streams in Nebraska and Kansas: Blue Creek, ●; Niobrara River, ○; North Loup River, ▼; and West Branch Mill Creek, △. Note that the number of sampled reaches required to detect 100% of total segment richness was greater than 10 (i.e., unknown and missing from plot) for all streams except West Branch Mill Creek.



lengths ($F_{[3,144]} = 3.50$, $P = 0.02$) for 75% changes in CPUE. The number of sampled reaches (at $\beta = 0.80$) needed to detect 25%, 50%, and 75% changes in CPUE for North Loup River, West Branch Mill Creek, and Blue Creek did not differ ($P > 0.008$ after Bonferroni correction) and were greater than the number of sampled reaches required to detect changes for Niobrara River (Fig. 3). The number of sampled reaches needed to detect changes decreased as the length of sampled reach increased. However, the number of sampled reaches required to detect 25% and 50% changes in CPUE did not differ ($P > 0.008$) between reach lengths of 20, 40, and 60 MSWs and were less than the number of sampled reaches required for sampled reaches of lengths of 10 MSWs (Fig. 3). Overall, the number of sampled reaches needed to detect changes was high. Even for common species, the number of sampled reaches of lengths of 60 MSW required to detect a 75% change in CPUE of common species (at $\beta = 0.80$) was still greater than 25% for stream segments of 20–28 km in length.

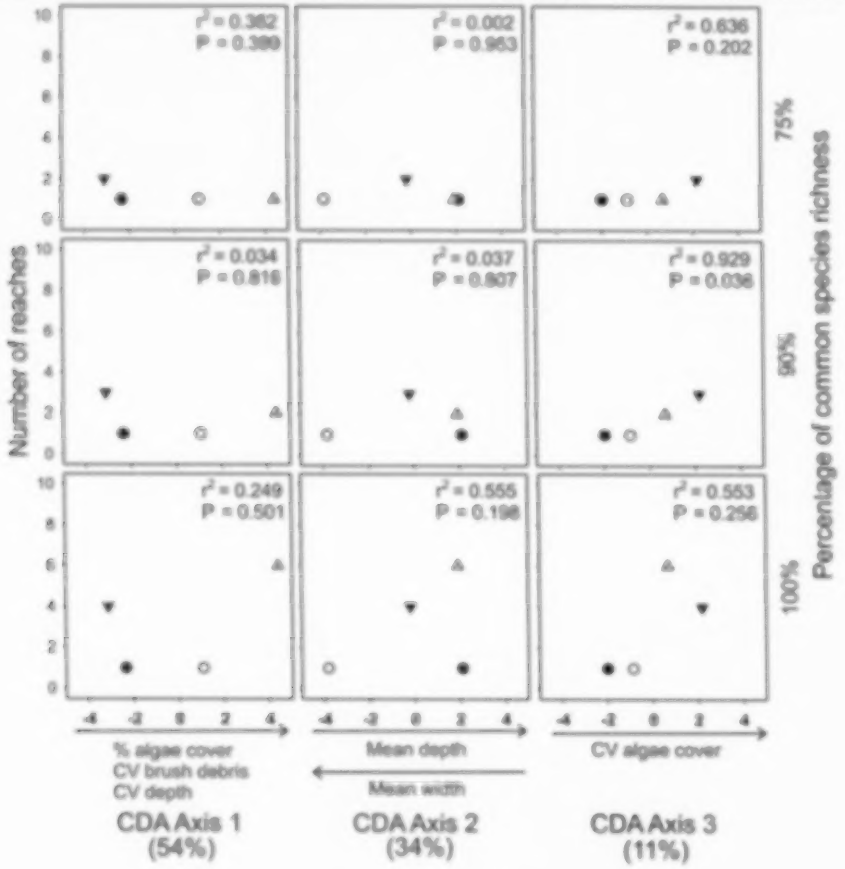
Species–area relationship

The observed rate of species accumulation (z) was calculated for all streams with sampled reach lengths combined (Fig. 4). The rate of species accumulation was lowest from sampled fish assemblages of North Loup River ($z = 0.07$), followed by West Branch Mill Creek ($z = 0.12$). The rate was similar for samples from Blue Creek and Niobrara River ($zs = 0.22$) and was greater than those observed from North Loup River and West Branch of Mill Creek.

Fish assemblage structure

Jaccard's similarity of sampled fish assemblages decreased as the distance between sampled reaches increased for all streams (Fig. 5). The relationship between Jaccard's similarity coefficients and the number of reaches between sampled reaches was more variable in Blue Creek ($r^2 = 0.10$) and Niobrara River ($r^2 = 0.11$) than in North Loup River ($r^2 = 0.31$) and West Branch Mill Creek ($r^2 = 0.33$). There was no difference in the rates of assemblage similar-

Fig. 7. Relationship between the number of sampled reaches of lengths equal to 40 mean stream widths required to detect 75%, 90%, and 100% of common segment species richness (i.e., species accounting for <1% of the cumulative catch for a stream segment removed) with a 95% probability and the mean canonical coefficients from the canonical discriminant analysis (CDA) of 24 habitat surveys from four mid-sized streams in Nebraska and Kansas: Blue Creek, ●; Niobrara River, ○; North Loup River, ▼; and West Branch Mill Creek, △.



ity decrease by distance among streams ($F_{[3,172]}$ = 1.72, P = 0.16), but rates of similarity decrease tended to be greater for sampled fish assemblages of North Loup River (–0.03) and West Branch Mill Creek (–0.02) than for sampled fish assemblages of Blue Creek (–0.01) and Niobrara River (–0.01). A negative correlation of sampled fish assemblage similarity and distance between reaches was observed in all streams except the Niobrara River (Mantel test, r = –0.26, P = 0.06). A weak correlation existed for the Blue Creek assemblage (Mantel test, r = –0.37, P < 0.01), whereas assemblages of North Loup River (Mantel test, r = –0.55, P < 0.01) and West Branch Mill Creek (Mantel test, r = –0.66, P < 0.01) had greater decrease in fish assemblage similarity as distance between sampled reaches increased. Greater fish assemblage similarity existed among sampled reaches of Blue Creek and Niobrara River, whereas North Loup River and West Branch Mill Creek exhibited less fish assemblage similarity among all sampled reaches.

Habitat associations

Stream width, depth, and percent cover of filamentous algae, depth CV, percent cover of filamentous algae CV, and percent cover of brushy debris CV discriminated among streams (Ps < 0.05). Three axes of the CDA were significant (Ps < 0.05) (Figs. 6 and 7). The first canonical axis accounted for 54% of total variability and was a gradient of percent cover of filamentous algae, CV of small woody debris percent cover, and CV of depth. Mean width and mean depth had the highest loadings on the second canonical axis and explained 34% of the total variability. The CV of filamentous algae percent cover was the only variable with a high loading on the third axis, which explained 11% of the total variation, and separated North Loup River and West Branch Mill Creek from streams with less variability in the percent cover of filamentous algae. The relationship of the mean standardized canonical axis scores of the first and second canonical axes and the number of sampled reaches needed to obtain 75%, 90%, and 100% of total (Fig. 6) and common species (Fig. 7) richness for each stream were not significant (Ps > 0.10). The relationships of the mean canonical axis scores of the third canonical axis and the number of sampled reaches needed to detect 75% and 90% of total spe-

cies richness were significant ($P = 0.09$ and 0.04, respectively) and negative ($\beta = -1.43$ and -0.85, respectively), indicating that as CV of filamentous algae increased, the number of sampled reaches needed to detect 75% and 90% of segment species richness decreased. After removal of rare species, the relationship between the third mean canonical axis scores and the number of sampled reaches needed to detect 75% of common species was the only significant relationship (Fig. 7; $P = 0.04$). This relationship was positive ($\beta = 1.83$), which indicates that by removing rare species, fewer sampled reaches were required with increased variation of filamentous algae cover.

Discussion

The ability to precisely estimate species richness at stream-segment spatial scales and detect changes in abundances of species over time has important implications for the conservation and management of stream fish assemblages. Overall, the four Great Plains streams sampled in our study represented a diversity of species richness, habitat, and assemblage structure. Moreover, the sampling effort needed for precise estimates of segment species richness and abundance differed among streams and habitat complexity. Despite these differences, our results suggested that consistent patterns of required sampling effort were influenced by fish assemblage and habitat structure within streams. We believe that our results provide a framework for researchers to develop and revise protocols for wadeable stream fish assemblage sampling across stream-segment spatial scales.

Our results suggested that moderate levels (i.e., 75%) of segment species richness are only obtainable after sampling three to five reaches with lengths equal to the widely accepted protocol of 40 MSWs (Peck et al. 2006) and more accurate levels (i.e., 90%) of segment species richness were only obtained after an extensive number of sampled reaches (i.e., six to 10 sampled reaches of lengths equal to 40 MSW) in relatively small stream segments of 20–28 km. However, because the total sampling effort required (cumulative MSWs) was consistently greater for longer sampled reaches, an increased number of shorter sample reaches would characterize stream segments with less total effort. The effort required to obtain segment species richness was consistently higher in Niobrara River and Blue Creek and consistently lower in West Branch Mill Creek and North Loup River, suggesting that stream characteristics (e.g., habitat complexity) affected sampling variability. Our results from Great Plains streams indicated that more homogeneous streams require more sampling effort to characterize fish assemblage structure, which is consistent with findings in streams from Illinois and Virginia (Angermeier and Smogor 1995). The failure of all four stream simulations to reach asymptotic levels of segment species richness suggests that there are discontinuous distributions or low densities for some species (Angermeier and Smogor 1995; Paller 1995), which was minimized after the removal of rare species. A species probability of occurrence in the available habitat is strongly correlated to the species relative abundance (Angermeier and Smogor 1995), suggesting that rare species are less likely to occupy all available habitats, which decreases the chance of being collected in a single sample.

The number of sampled reaches required to obtain precise estimates of common species richness for the entire segment were consistently lower for Niobrara River and Blue Creek and higher for North Loup River and West Branch Mill Creek simulations. The increased number of sampled reaches needed to collect estimates of species richness within Niobrara River and Blue Creek when all species were included was likely caused by rare species, which were not sampled at a majority of sampled reaches. Although total segment species richness may not be a feasible objective, sampling effort decreased considerably when only common species were considered and would be much more reasonable to most managers and researchers of similar systems if common species were the focus of the study objectives. Our findings suggested that well-established standardized protocols used by agencies for monitoring fish assemblages and their responses to environmental change may not accurately characterize fish assemblages at larger spatial scales and may fail to catch species of low relative abundance within an individual stream segment.

Overall, a large number of sampled reaches would be needed to detect trends in the relative abundance of common stream fishes in the four Great Plains streams sampled, which is similar to other studies in rivers and streams (Peterson and Rabeni 1995; Paukert 2004; Quist et al. 2006). However, unlike other studies of sample size estimation, we determined that increasing sampled reach length decreased the number of sampled reaches needed to detect trends in relative abundance of fish species. This suggests that longer sampled reaches decreased variability in CPUE for common species. However, increasing the length of sampled reaches beyond 20 MSWs did not decrease the number of sampled reaches required to detect changes in CPUE. A similar pattern in the number of sampled reaches needed to obtain varying levels of total segment species richness estimates was observed in the estimated number of sampled reaches needed to detect trends in CPUE. Streams with greater habitat complexity and less overall assemblage similarity between sampled reaches required more sampled reaches to detect trends in CPUE than streams with less habitat complexity and greater similarity of sampled fish assemblages. Because only common species were used in the sample size estimates, our results indicated that greater variability in CPUE may be influenced by increased habitat complexity and were not a result of discontinuous distributions of rare species, which is in contrast to findings by Angermeier and Smogor (1995).

The species–area relationship has been well established over the last century (Arrhenius 1921; Williams 1964; Rosenzweig 1995) and has been the foundation of many studies focused on determining the balance between inaccurately characterizing assemblages by undersampling and cost-prohibitive oversampling. Although increasing sampling area and encountering more species may be the result of more effectively sampling the available species (Connor and McCoy 1979), increasing sampling area may also increase the habitat diversity sampled, which can support a greater number of species (Williams 1964; Cam et al. 2002). Within our study streams, the rate of species accumulation differed among streams but apparently was not affected by stream species richness. This may suggest that

the relationship between species and area may not be attributable strictly to sampling phenomena but is likely a combination of habitat complexity, species distributions, and sampling (Angermeier and Schlosser 1989). Additionally, our results from the species–area relationships were consistent with the effort required to obtain various levels of segment richness among streams. For example, Niobrara River and Blue Creek required consistently less effort than North Loup River and West Branch Mill Creek, further suggesting that habitat complexity and species distributions contributed to the differing rates of species accumulation, which is similar to findings of Angermeier and Smogor (1995). In contrast, other studies of species accumulations and sampling effort have found varying effects of habitat. Weak or uncorrelated habitat effects were found by Lyons (1992), Hughes et al. (2002), and Smith and Jones (2005), whereas Paller (1995) and Dauwalter and Pert (2003) found stream size best explained differences in sampling efforts.

Fish assemblage similarity increases with decreased distances between samples and is related to the physical habitat that changes as streams increase in size (Platania 1991; Rahel and Hubert 1991; Edds 1993). Based on our data, assemblage similarity of sampled reaches was related to the number of sampled reaches required for precise estimates of species richness and the ability to detect trends in CPUE. Niobrara River and Blue Creek exhibited lower rates of dissimilarity between samples and greater variation among all sampled reaches than North Loup River and West Branch Mill Creek. Greater rates in these relationships indicate an increased rate of species turnover (i.e., increased dissimilarity as the distance between sampled reaches increases) among all sampled reaches. Additionally, greater variability in Jaccard's similarity of sampled fish assemblages indicated that samples from reaches with a greater likelihood for increased similarity (i.e., sampled reaches in closer proximity to each other) were less likely to be similar, whereas sampled reaches with greater distances between samples had greater assemblage similarity. This is likely due to species (e.g., rare or habitat specialists) that were not consistently sampled at all reaches within a segment. Our results suggested that stream segments with less similar assemblages among all reaches (i.e., North Loup River and West Branch Mill Creek) required fewer sampled reaches to achieve the same proportion of species richness than streams that had more similar assemblages among sampled reaches within the entire segment (i.e., Blue Creek and Niobrara River). Therefore, the random selection of sampled reaches with less similar fish assemblages represented a greater proportion of the stream-segment species richness (i.e., autosimilarity; Cao et al. 2002). Streams with higher species turnover (e.g., low similarity between sampled reaches) should require fewer systematically sampled reaches to characterize a greater proportion of species in the segment than streams with more similar assemblages (Cao et al. 2001). Overall, our results of Jaccard's similarity of fish assemblage samples within streams suggested that given a fixed number of samples to characterize a stream segment, a greater distance between sampled reaches would represent a greater percentage of the segment assemblage.

The increased number of sampled reaches needed to obtain a given proportion of segment species richness in streams with higher variation in percent cover of filamentous algae is likely due to rare species discontinuous distributions and habitat selectivity (Angermeier and Smogor 1995). Because habitat complexity was lower in the streams that required a greater number of sampled reaches to obtain similar estimates of total segment species richness, rare species may be selective to specific habitat types, thus resulting in low overall relative abundances and infrequent collection throughout sampling segments. Stream segments with greater habitat homogeneity present fewer opportunities for rare species to be collected, which in turn may increase the number of sampled reaches needed to collect all species present. Additionally, Angermeier and Schlosser (1989) found that habitat complexity was correlated to species richness in Panama streams but not in streams in Minnesota and Illinois and suggested that the greater stability of streams in Panama may facilitate this relationship. Larger streams with greater habitat heterogeneity and less temporal variation typically have stable fish assemblages (Schlosser 1987). The four midsized Great Plains streams sampled in our study may be better suited for evaluating assemblage variability as related to habitat within stream segments because of their larger and more stable flow regimes relative to smaller streams.

Although a number of studies have described the length of sampled reach needed (number of MSWs) to describe stream fish assemblages within reaches (e.g., Lyons 1992; Patton et al. 2000; Reynolds et al. 2003), our results indicated that multiple sampled reaches within a segment are needed to characterize stream fish assemblages. To our knowledge, only one other study (i.e., Smith and Jones 2005) has evaluated the sampling effort (i.e., with multiple reaches) required to estimate species richness at large spatial extents. Results from Smith and Jones (2005) suggest that 15–119 sampled reaches of lengths equal to 30 MSW were needed to characterize Great Lakes watersheds but found no environmental or assemblage correlates to the required sampling effort. Our results suggested that the number of sampled stream reaches required in Great Plains streams to estimate species richness may not be cost effective because of discontinuous species distributions or low species abundance (40% of the species in our study streams represented less than 4% of the total number of individuals collected in each stream). However, 75% of all fish species were obtained with the least amount of total effort with five to 10 sampled reaches with lengths equal to 20 MSW for all four streams. Monitoring changes in common species relative abundance in Great Plains streams may require an even greater increase in sampling effort. The number of sampled reaches needed to detect presences and monitor changes in relative abundances of stream fishes will ultimately depend on individual study objectives and the scale to which stream fish assemblages are to be characterized. Our results suggested that the sampling effort needed to characterize streams could be decreased by evaluating instream habitat characteristics. Furthermore, previous knowledge of stream fish assemblage structure and species abundances may assist in the establishment of required sampling effort and in determining areas needing additional sampling effort to characterize a greater proportion of species present.

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The relative weight of traditions, economics, and catch plans in New Zealand fleet dynamics

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Abstract: We investigate the relative weights of catch plans, expected profit, and traditions in fishers' decision-making for five New Zealand fleets subject to an individual transferable quota (ITQ) management regime. Métiers were defined for these fleets as a combination of gears, management units, and a targeting index (either target species or statistical area). A nested logit random utility model was used to model the métier allocation of fishing effort in relation to catch plans, expected profit, and past fishing allocations. This study showed that traditions and catch plans appeared to be important determinants of fishers' behavior for these New Zealand fleets. The model developed in this study fitted the data generally well and was also able to predict, in most cases, future effort allocation both one month and one year ahead.

Résumé : Nous étudions le poids relatif des portefeuilles de captures, du profit attendu et des traditions dans le processus de prise de décision des pêcheurs, dans le cas de six flottilles néo-zélandaises gérées par des quotas individuels transférables (ITQ). Plusieurs métiers ont été définis pour ces flottilles, en utilisant une combinaison des engins de pêche, des unités de gestion et d'?un indice de ciblage (soit les espèces recherchées ou les régions statistiques). Un modèle de choix discrets imbriqué (« random utility model ») a été utilisé pour modéliser l'allocation de l'effort de pêche en métiers, en utilisant les plans de pêche, le profit attendu et les allocations de pêche passées comme variables explicatives. Nous montrons que les traditions et les plans de pêche sont d'importants déterminants du comportement de pêche dans le cas des flottilles néo-zélandaises étudiées. Le modèle développé dans cette étude est bien calibré par les données disponibles et peut permettre dans la plupart des cas de prévoir raisonnablement quelle sera l'allocation de l'effort de pêche un mois, et même un an à l'avance.

Introduction

Fleet dynamics, the key process bridging fisheries decision-makers and fish resources, has been subject to increased attention by the scientific community over the past 25 years (Hilborn 1985; Gillis 2003; Branch et al. 2006*a*). Research to date has focused mainly on the mechanisms of (*i*) effort allocation (Gillis et al. 1993; Holland and Sutinen 1999; Poos and Rijnsdorp 2007), (*ii*) entering and exiting fisheries (Bockstael and Opaluch 1984; Ikiara and Odink 1999; Pradhan and Leung 2004*b*), (*iii*) technological changes (Rahikainen and Kuikka 2002; Kirkley et al. 2004; Marchal et al. 2007*a*), (*iv*) discarding (Gillis et al. 1995; Pascoe and Revill 2004), and (*v*) compliance (Raakjaer Nielsen and Mathiesen 2003).

In particular, in recent years, the processes underlying the dynamics of effort allocation have been investigated through a number of research projects conducted by fisheries biologists and (or) economists (Reeves et al. 2008). This has been driven to a large extent by an increasing interest in the implementation of area-based fisheries management (Hutton et al. 2004; Murawski et al. 2005; Poos and Rijnsdorp 2007), but also in the context of fishers' reactions to pollution events such as an oil spill (Collins et al. 2003).

Fishers' location choices may also be driven by available fishing opportunities, which reflect the relative quantity of each species (or stocks) that they are entitled, or are incentivised, to catch. This is particularly true in management systems that include individual transferable quota (ITQ), which provide individual fishers or fishing companies with a share of the overall total allowable catch (TAC) for each stock (Arnason 1993; Sanchirico et al. 2006).

In theory, ITQs create incentives for fishers to maximize the value of their catch and minimize harvest costs. They also create, in principle, economic incentives to avoid catch of species for which the fisher does not have quota. In mixed-species ITQ fisheries, fishers have a portfolio of catch rights, the catch plan. They are expected to operate their fishing operations in such a way that their resulting catch mix matches their catch plan as much as possible. However, it is almost inevitable that fishers' species mix of catch will not match exactly their portfolio of catch rights (Annala et al. 1991; Branch et al. 2006*b*). First, even when fishers want to conform to their catch plan, they may, at the same time, want to achieve alternative objectives (e.g., maximizing profit, fishing according to traditions). Because these objectives may prove difficult to reconcile, their combination may lead to a mismatch between the fishers' catch mix and their species portfolio. Second, uncertainty (due to, e.g., stock fluctuations or unforeseen weather conditions) is

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usually an ingredient of fishing operations, which may cause fishing outcomes, including catch composition, to differ substantially from initial expectations.

A number of bioeconomic analyses have been carried out in relation to the impact of ITQ on biological sustainability, economic efficiency (Sigler and Lunsford 2001; Holland et al. 2005; Holland and Herrera 2006), and discarding practices (Branch 2006; Branch et al. 2006*b*). However, to our best knowledge, none of these studies has investigated the effects of individual catch rights on fishers' behavior. In the existing literature, fishers' behavior has been modeled in relation to maximizing expected profit or catch rates (Vignaux 1996; Dorn 2001; Salas et al. 2004), sometimes also in combination with traditions and (or) area closures (Holland 2000; Hutton et al. 2004; Poos and Rijnsdorp 2007). The approaches pursued to model fishers' behavior have included random utility models (RUMs) (Holland and Sutinen 1999; Hutton et al. 2004; Pradhan and Leung 2004*a*), random walks (Bertrand et al. 2005; Marchal et al. 2007*b*), dynamic programming (Babcock and Pikitch 2000), and the application of theoretical concepts such as ideal free distribution theory (Gillis et al. 1993; Rijnsdorp et al. 2000; Abernethy et al. 2007) and game theory (Trisak 2005).

The main objective of this study is to investigate the relative importance of catch plans, economics, and traditions in fishers' decision-making for five New Zealand fleets regulated by ITQs. One of these fleets mainly targets hoki (*Macruronus novaezelandiae*), whereas the others mainly target snapper (*Pagrus auratus*). We describe the background of the case studies, characterize the five fleets being investigated and the different métiers (or fishing activities) they operate, and derive an estimate of fishers' catch plans based on available data. We then apply a RUM to model and predict fishers' decision-making. A number of explanatory variables are investigated, and these are related to the fishers' catch portfolio, economics, and traditions.

Background

Management

The main management framework of New Zealand fisheries is the quota management system (QMS), which has been in use since 1986 (Batstone and Sharp 1999; Bess and Harte 2000; Hersoug 2002). For each stock managed under the QMS, a TAC is set at the beginning of the fishing year by the Minister of Fisheries, advised by the Ministry of Fisheries, mainly on the basis of ensuring stocks remain at or above a level capable of producing the maximum sustainable yield. For most New Zealand stocks, including those harvested by the fisheries investigated here, the fishing year n starts on 1 October in year $n - 1$ and ends on 30 September in year n. TACs are then allocated to (*i*) customary (Maori) and recreational fishers, (*ii*) a virtual compartment including mainly illegal fishing, and (*iii*) the commercial fishing sector. The shares of the TACs allocated to the commercial fishing sector are referred to as the total allowable commercial catches (TACC). TACCs are distributed to quota holders as ITQ shares. On the first day of the fishing year, each ITQ (expressed as a percentage of the TACC) generates for each quota holder, and each stock, a catching right (in kilograms) referred to as the annual catch entitlement (ACE), so that

$$\mathrm{ACE(kg)} = \mathrm{TACC(kg)} \times \mathrm{ITQ(\%)}$$

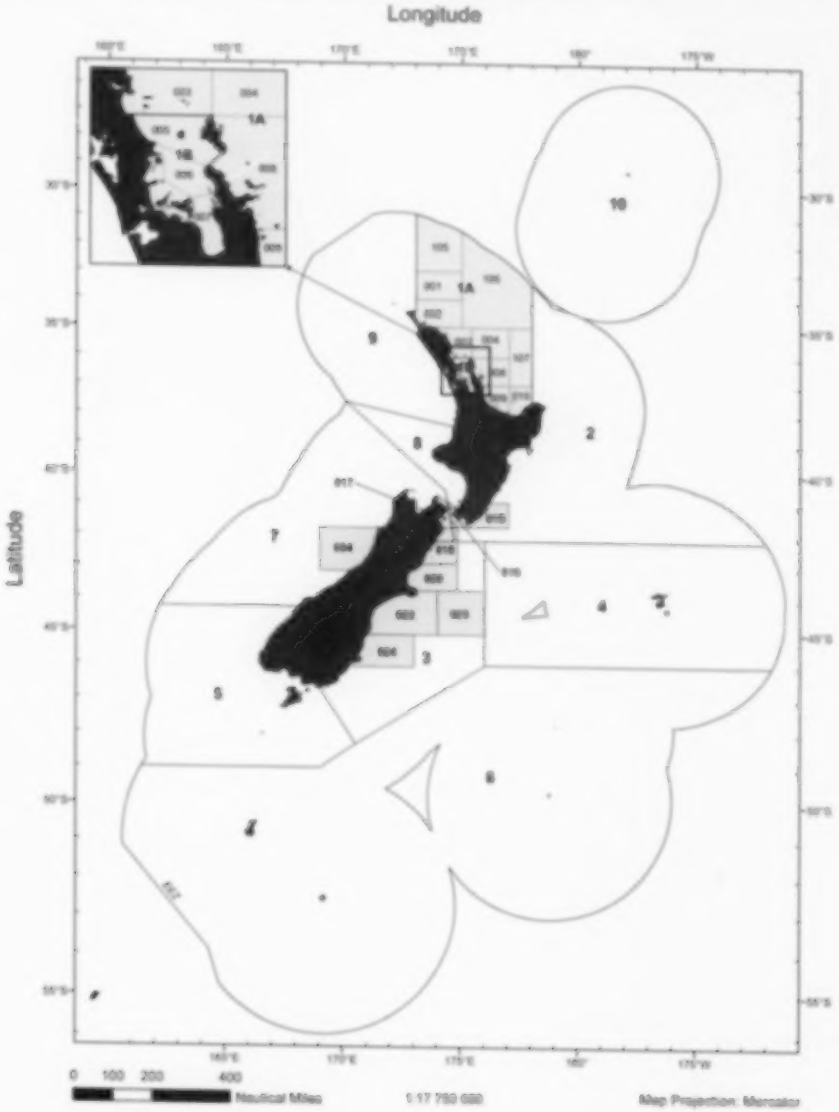
ACE, like ITQ, is freely tradable on the open market. Despite that flexibility, and even where fishers are allowed to acquire catch rights after landing fish, aggregate commercial catches may not always match up with TACCs. Discarding is prohibited in New Zealand for almost all species managed under the QMS, but fishers are allowed to land species in excess of their ACE, even when the overall TACC for these species has been exceeded already. In that case, at the end of the fishing year, fishers are charged a fee, or "deemed value", for each unit of catch that they land above their ACE holdings at the time. The deemed value is set annually by the Minister of Fisheries, advised by the Ministry of Fisheries, at the same time as the TAC and the TACC. There is no clear policy or rationale as to how the deemed value is calculated. However, the level at which the deemed value is set may have dramatic consequences for the fisheries sustainability. Although a high deemed value (i.e., well above the ACE price) may encourage fishers to shift target species when ACE is in short supply on the market, a deemed value set at a low level (i.e., close to or below the ACE price) may incite fishers to pay the charge requested and continue targeting the same stock, even when they have no ACE. For instance, the deemed value for hoki has been lower than the ACE price in 2007, and the TAC set for that stock was exceeded at the end of the fishing year.

The case studies

This study focuses on five fisheries case studies, one is a hoki fishery and the other four are northern snapper fisheries operated by different fleets. The hoki fishery was initially developed by Japanese and Soviet vessels in the early 1970s on the hoki spawning areas off the west coast of South Island from mid-July to late August. The fishery has expanded since the late 1980s on separate spawning aggregations located in Cook Strait, the east coast of the South Island, and at Puysegur Bank. Hoki catches are capped by one single TACC, which covers most of the New Zealand EEZ. In addition, following an informal agreement between the Minister of Fisheries and the industry, an allocation key is defined to split the TACC between the eastern and the western stock areas. In the mid-1990s, both the TACC and catches were around 250 000 tonnes (t). Since 2000, successive reductions have led to a TACC of 100 000 t in 2008. The hoki fishery is mainly operated by large vessels with bottom trawls and, to a lesser extent, midwater trawls. At the scale of a fishing operation (haul), the main commercial bycatch species are hake (*Merluccius australis*), ling (*Genypterus blacodes*), and silver warehou (*Seriolella punctata*). At the scale of a fishing trip, or of a fishing year, vessels involved in the hoki fishery may also target squids (*Nototodarus gouldi*, *Nototodarus sloanii*), barracouta (*Thyrsites atun*), and other species.

Snapper fisheries are among the most valuable coastal fisheries in New Zealand. The snapper stock harvested off the east coast of North Island (hereby referred to as the northern snapper) is the most important of the five snapper stocks in New Zealand waters (Fig. 1). Since the inception

Fig. 1. Map of New Zealand management units and of the main statistical areas relevant to the hoki fishery (fleet 1, in blue) and the northern snapper fishery (fleets 2–5, in salmon). The insert expands the Bay of Plenty. The large-sized, one- or two-digit numbers refer to the management units; the small-sized, three-digit numbers refer to the statistical areas.



of the QMS in 1986, the northern snapper commercial catches have fluctuated between 4000 and 6000 t. The TACC has been set at 4500 t since 1997. An important feature of the northern snapper fishery is the relatively large quantity of recreational and customary catches. The northern snapper fishery is mainly operated by small vessels (<24 m) fishing inshore with longlines, bottom trawls, and to a lesser extent, Danish seines and fixed nets. The longline fishery is mostly single species, with snapper contributing more than 90% of the total catches. The main commercial bycatch species of the bottom trawl and Danish seine fisheries are, in various proportions, barracouta, flatfish, gurnard (*Chelidonichtys kumu*), John Dory (*Zeus faber*), kahawai (*Arripis trutta*), kingfish (*Seriola lalandi*), leatherjacket (*Parika scaber*), blue moki (*Latridopsis ciliaris*), tarakihi (*Nemadactylus macropterus*), and trevally (*Pseudocaranx dentex*). Of importance to the present investigation is the Bay of Plenty (Fig. 1). Fishing in the Bay of Plenty is subject to specific management regulations, including seasonal closures and limited use of trawling.

Table 1. Fleets and métiers investigated.

Fleets			Métiers					
Code	Description	N_f	Main gears	Main management units	Type	N_m	Targeting index	Targeting index values
1	Hoki trawlers	28	Bottom and midwater trawl	2, 3, 7	1	6	Main target species	Hoki, barracouta, red cod, squid
					2	8	Main statistical areas	015, 016, 017, 018, 020, 022, 023, 024, 034
2	Snapper longliners (<12 m)	28	Bottom longline	1A, 1B	1	5	Main target species	Snapper
					2	9	Main statistical areas	002, 003, 005, 006, 007, 008, 009
3	Snapper longliners (12–24 m)	28	Bottom longline	1A, 1B	1	5	Main target species	Snapper
					2	7	Main statistical areas	002, 003, 005, 006, 007, 008, 009, 010
4	Snapper bottom trawlers	37	Bottom trawl	1A, 1B	1	10	Main target species	Gurnard, John Dory, snapper, tarakihi, trevally
					2	8	Main statistical areas	003, 005, 008, 009, 010
5	Snapper Danish seiners	27	Danish seine	1A, 1B	1	7	Main target species	Gurnard, John Dory, snapper
					2	8	Main statistical areas	005, 006, 007, 008, 009, 010

Note: Métiers are described in terms of main gears, management units, and either target species (métier type 1) or statistical areas (métier type 2). N_f is the total number of métiers for each fleet; N_m is the total number of métiers for each fleet and each typology. The main target species are barracouta (*Thyrsites atun*), gurnard (*Chelidonichtys kumu*), John Dory (*Zeus faber*), hoki (*Macruronus novaezelandiae*), red cod (*Pseudophycis bachus*), snapper (*Pagrus auratus*), squids (*Nototodarus* sp.), tarakihi (*Nemadactylus macropterus*), and trevally (*Pseudocaranx dentex*).

Material and methods

Fleets and métiers

Fleets

Consistent with International Council for the Exploration of the Sea (ICES) (2003), a fleet was defined as a group of vessels of a certain size targeting a given group of species with a specific gear and, in the case of the northern snapper fishery, fishing in management units 1A and 1B (Fig. 1) in at least 50% of the days fished throughout a given year.

For the hoki middle-depth fishery, the fleet investigated (fleet 1) consisted of bottom trawlers targeting hoki, hake, ling, silver warehou, squids, and barracuta. Only vessels below 46 m were included in the analysis. The 46 m cutoff was chosen because trawlers above that size are not allowed to fish within the 12 nautical mile territorial sea boundary (i.e., inshore waters) (Table 1).

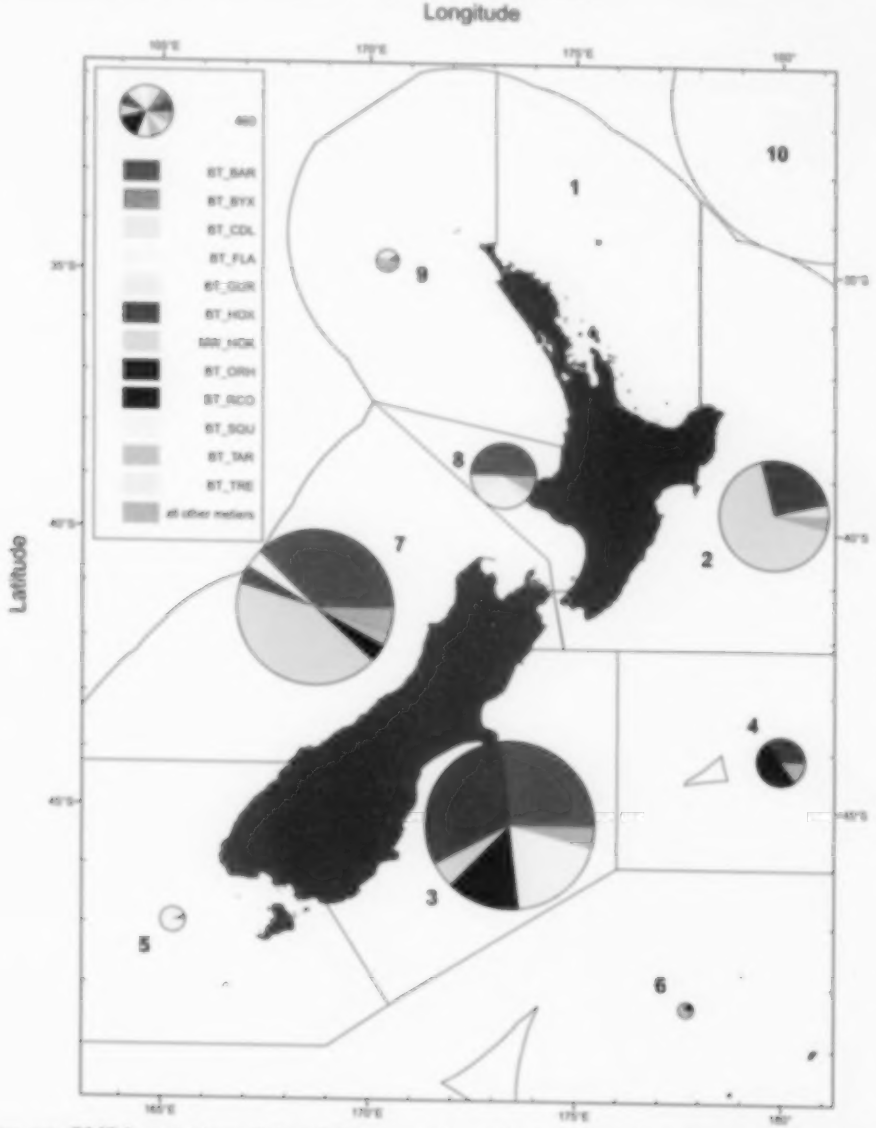
For northern snapper fisheries, the main gears used were longlines, bottom trawls, and Danish seines, and the main target species were snapper, gurnard, John Dory, kahawai, tarakihi, or trevally in the management units 1A and 1B. Four fleets were then identified (Table 1): longliners below 12 m (fleet 2), longliners of length 12–24 m (fleet 3), bottom trawlers of length 12–24 m (fleet 4), and Danish seiners smaller than 24 m (fleet 5).

Métiers

Each fleet may operate different métiers, or fishing activities, throughout the year. Métiers may be characterized by a number of factors including target species, gears, statistical areas, and management units. In our study, all decisions and, most particularly, métier choices were modeled at the scale of a fishing trip. The different métier characteristics (target species, gears, statistical areas, management units) could, in principle, be altered within a trip. In such cases, we used the most commonly reported value for these factors during that trip. For instance, if a fisher targeted hoki and squid during 80% and 20%, respectively, of the days fished within one fishing trip, then the target species associated with that trip would be hoki. In case of a tie, we selected the factor's value leading to the largest total catch; for example, if during a trip, a fisher dedicated exactly the same amount of time to targeting hoki and squid and caught in total 300 kg and 200 kg, respectively, of fish when targeting these species, the target species associated with that particular trip would be hoki.

Two métier types have been tested in this study. Both métier types combine a gear, a management unit, and a targeting index. The New Zealand QMS is based on 10 management units (1–10). In this study, we considered 11 management units, of which nine are consistent with the QMS (2–10) and two consist of a subdivision of management unit 1 into 1A (outside the Bay of Plenty) and 1B (inside the Bay of Plenty) (Fig. 1). The rationale for distinguishing management units 1A and 1B is that specific regulations apply in the Bay of Plenty. With métier type 1, the targeting index is the main target species as reported in the fishers' logbooks, so an example of a type 1 métier could be bottom trawling in management unit 1A and targeting snapper. With métier type 2, the targeting index is the main statistical area visited by fishers during a fishing trip.

Fig. 2. Spatial distribution of fishing effort for fleet 1 (hoki bottom trawlers) by métier using typology 1. Codes: BT_BAR, bottom trawl barracouta (*Thyrsites atun*); BT_BYX, bottom trawl alfonsino (*Beryx* spp.); BT_CDL, bottom trawl black cardinal fish (*Epigonus telescopus*); BT_FLA, bottom trawl flatfish (various species); BT_GUR, bottom trawl gurnard (*Chelidonichtys kumu*); BT_HOK, bottom trawl hoki (*Macruronus novaezelandiae*); MW_HOK, midwater-trawl hoki; BT_ORH, bottom-trawl orange roughy (*Hoplostethus atlanticus*); BT_RCO, bottom-trawl red cod (*Pseudophycis bachus*); BT_SQU, bottom-trawl squid (*Nototodarus* spp.); BT_TAR, bottom-trawl tarakihi (*Nemadactylus macropterus*); BT_TRE, bottom-trawl trevally (*Pseudocaranx dentex*).



Statistical areas are QMS-based, three-digit subdivisions of the management units defined above. An example of a type 2 métier could be midwater trawling in management unit 2 and in statistical area 015. To keep the number of métiers tractable and to limit the number of missing values, for both typologies, we aggregated the least frequent (used in less than 5% of the fishing trips) management units, gears, and targeting indices into one single "other" category. The métiers identified, using the two typologies, are shown for the five fleets under investigation (Table 1). The spatial distribution of fishing effort by fleet and by métier is also shown, using both typologies (Figs. 2 and 3).

Data

Catch and effort

Relevant catch and effort data, collected in New Zealand logbooks for the period 2001–2006, were provided by the Ministry of Fisheries for our study. Landing data were reported by fishing trip and statistical area. Fishing effort data

were provided by gear, target species, and fishing event. For example, one tow, or one set, and all of its associated effort data constitute a fishing event. The number of days at sea was used as a proxy for fishing effort for all fleets being investigated. More detailed and specific metrics could have been considered to characterize the fishing effort associated with particular gears (e.g., number of hours fished for trawlers, number of hooks soaked for longliners); however, using such metrics would not allow comparing the fishing effort, or any variable derived from fishing effort, of métiers when these are using different gears. Using the number of days at sea allowed comparing fishing effort across the métiers operated by each fleet, even when different gears are used. The landing and effort table eventually used in the analysis was aggregated at the level of the fishing trip. Each fishing trip was linked to a quota holder, which could be the fisher or a quota holding company that contracts the fisher for that fishing trip.

ACE holdings and trading prices

For the purpose of this study, quarterly ACE holdings and trading prices were extracted from ACE and quota share registers for each stock and quota holder of interest over the period 2001–2006. The quarterly ACE holdings were calculated from the initial ACE holdings allocated at the start of the fishing year corrected by the net amount of ACE traded (i.e., purchases minus sales) during that quarter. ACE holdings and trading prices were linked to catch and effort by year, quarter, and quota holder.

Fish prices

The only source of information available on fish prices is from a survey that collects prices paid by licensed fish receivers to fishers. This survey has been conducted annually by the Ministry of Fisheries and is used to calculate the levy charged to quota holders for the costs of fisheries management and scientific advice (e.g., stock assessments). Discussions with industry representatives suggested, however, that fish prices may include three elements of bias. First, it is uncertain whether the prices reported by licensed fish receivers include only the transaction prices or whether some costs associated with the fishing activity or the ACE rental have been deducted. Second, the surveyed prices are used to calculate a cost-recovery levy and this may generate an incentive to report low prices. Third, because the survey is conducted annually, there are no estimates of seasonal prices. As no better information was available, we used the fish price data collected during the survey. The possible implications of using such data have been addressed in the Methods section and in the Discussion.

Deemed value

Annual deemed values were available from the Ministry of Fisheries for all fish stocks under investigation. Some of these stocks are subject to a flat deemed-value rate, i.e., a rate unchanged irrespective of the quantity of fish caught over the ACE. Other stocks, however, including hoki (since October 2003) and northern snapper, have a differential deemed-value rate, which increases stepwise with the proportion of catches landed above the ACE.

Relative expected catches

In ITQ systems, fishers usually have catch plans. In New Zealand, catch plan information data are not available to the general public, and discussions with industry representatives were organized to collect such data. Most of the hoki and northern snapper ACEs are held by quota holding companies. We planned to interview representatives of the companies holding the greatest proportion of ACEs for the two stocks. For both stocks, more than 50% of the TACC (4586 t) was held by only three companies in fishing year 2006. In total, we conducted interviews with representatives of four companies, which represented 30% and 20% of the ACE holdings of hoki and northern snapper, respectively. All the interviews were conducted between September 2007 and January 2008.

The discussions with the representatives of these companies suggested that catch plans were set before the start of the fishing year for each vessel or vessel size category and subject to adjustments throughout the fishing year. It was also suggested that the proportional contribution of each species in individual vessels' catch plans was fairly stable throughout the period investigated here. Two of the four interviewed representatives also provided quantitative information, which could be used as a basis to estimate catch plans for the hoki and snapper fisheries. This information was given in different formats, depending on the fleet being considered. For the hoki fleet, annual expected catches were supplied by vessel and fish stock (in tonnes) for three vessels (out of 28) from fishing year 2005 onwards. For the northern snapper fleets, monthly expected catches by vessel and fish stock (in tonnes) were supplied for eight vessels (out of 120) for fishing year 2007.

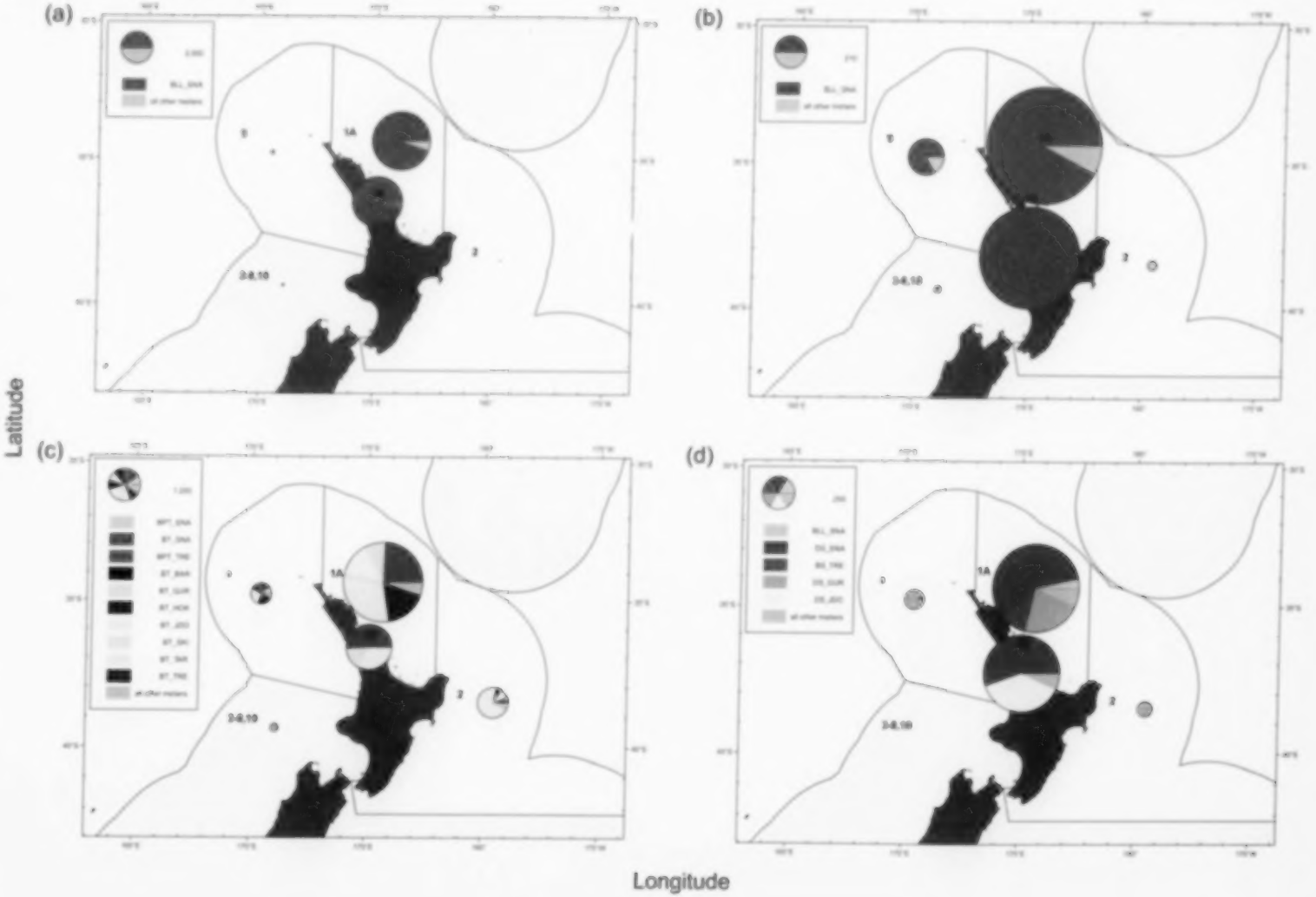
To make use of this information, we derived the relative expected catch as the proportional contribution of each species' expected catch to the total expected catch for all species. We then extrapolated the relative expected catch to all fishing vessels and fishing years. In doing this extrapolation, we made two assumptions. First, we assumed that fishing vessels for which information was provided were representative of, and therefore could be extrapolated to, the fleet to which they belonged. Second, consistent with discussions held with industry representatives, we assumed that expected catches were changed little over the period of investigation. Therefore, for fleet 1, we extrapolated the 2005 relative expected catches to fishing years 2002–2004. For fleets 2–5, we extrapolated the 2007 relative expected catches to all earlier fishing years.

Methods

Model structure

Random utility models (RUMs; McFadden 1974; Bockstael and Opaluch 1984; Holland and Sutinen 1999) have been used to model individual vessel choices. For each fleet, each individual vessel's skipper (v) may choose at the beginning of each fishing trip (i) among different métiers (alternatives) (m). Each alternative has a utility function associated with it, which may be interpreted here as the expected benefit (in a broad sense) that each individual derives from that alternative relative to other possible alternatives. The random utility function can be decomposed into deterministic

Fig. 3. Spatial distribution of fishing effort by métier, using typology 1, for the northern snapper fleets: (*a*) fleet 2 (small longliners); (*b*) fleet 3 (medium longliners); (*c*) fleet 4 (bottom trawlers); and (*d*) fleet 5 (Danish seiners). Codes: BLL_SNA, bottom longline snapper (*Pagrus auratus*); BPT_SNA, bottom pair trawl snapper; BT_SNA, bottom trawl snapper; BPT_TRE, bottom pair trawl trevally (*Pseudocaranx dentex*); BT_BAR, bottom trawl barracouta (*Thyrsites atun*); BT_GUR, bottom trawl gurnard (*Chelidonichtys kumu*); BT_HOK, bottom trawl hoki (*Macruronus novaezelandiae*); BT_JDO, bottom trawl John Dory (*Zeus faber*); BT_SKI, bottom trawl gemfish (*Rexea solandri*); BT_TAR, bottom trawl tarakihi (*Nemadactylus macropterus*); BT_TRE, bottom-trawl trevally (*Pseudocaranx dentex*); DS_SNA, Danish seine snapper; BS_TRE, beach seine trevally; DS_GUR, Danish seine gurnard; DS_JDO, Danish John Dory.



and stochastic components. Different distributions may be contemplated for the stochastic component, leading to different model types. We applied here a nested logit model, as it imposes a hierarchical structure that conceptually could accommodate the organization of the fishers' decision-making process (Holland and Sutinen 1999). The details on the structure of the RUM used in this investigation may be found in Appendix A. The methodology has been implemented using the MDC procedure of software package SAS (SAS Institute Inc., Cary, North Carolina).

Explanatory variables

A range of explanatory variables has been included in the model specification. Some of them (economics, risk management, tradition) are "usual suspect" variables, which have traditionally been used in a range of fisher behavior studies (Holland and Sutinen 1999; Hutton et al. 2004; Pradhan and Leung 2004*a*). Others, however, are specifically dedicated to explore how available catch plans affect fishers' behavior in mixed fisheries. To our best knowledge, such variables have never been investigated in past behavioral studies. We specify below the different explanatory variables and the levels at which they were introduced into the model structure.

Expected profit

We assumed here that the skipper of each individual vessel v on fishing trip i would estimate the expected monetary profit of choosing a given métier based on the most recent profit information and the profit from the same month in the previous year. Recent profit information was averaged over all vessels in the same fleet and all fishing trips in the same métier, as defined by the previous month's value per unit effort (VPUE). The seasonal component of VPUE was assumed to be related to VPUE 12 months previously averaged over all vessels belonging to each fleet. The seasonal component was necessary because a number of processes underlying the dynamics of profit, such as stock availability, fish prices, and ACE prices, are seasonal.

Because stock densities are subject to important spatial variations, we assumed that the VPUE in both the previous month and the previous year were taken into account mostly at the bottom decision level of the model structure.

We refer to the VPUE in the previous month and the VPUE in the previous year, respectively, as the short-term and the long-term VPUE, and these may be formulated as

$$\text{VPUE_1}_{f,m} = \text{VPUE}_{t-1,f,m} = \frac{1}{N_S N_f N_m} \sum_{s \in N_S} \sum_{v \in N_f} \sum_{i \in N_m} \left[\frac{(\pi_{t-1,s} - \chi_{t-1,s}) Y_{t-1,s,v,i}}{E_{t-1,v,i}} \right]$$

$$\text{VPUE_12}_{f,m} = \text{VPUE}_{t-12,f,m} = \frac{1}{N_S N_f N_m} \sum_{s \in N_S} \sum_{v \in N_f} \sum_{i \in N_m} \left[\frac{(\pi_{t-12,s} - \chi_{t-12,s}) Y_{t-12,s,v,i}}{E_{t-12,v,i}} \right]$$

where VPUE_1 is the short-term (or previous month) VPUE, VPUE_12 is the long-term (or previous year) VPUE, t is one month of the fishing period being investigated, s is a specific stock, f is a specific fleet, N_S is the number of stocks caught by vessel v during fishing trip i, N_f is the number of vessels belonging to fleet f, N_m is the number of fishing trips belonging to métier m, $Y_{t,s,v,i}$ is the yield (kg) obtained by vessel v during fishing trip i operated in month t for fish stock s, $E_{t,v,i}$ is the fishing effort (expressed in number of fishing operations) exerted by vessel v during fishing trip i operated in month t, $\pi_{t,s}$ is the price of fish stock s in month t, $\chi_{t,s}$ is the cost of renting an ACE, or paying the deemed value, for stock s in month t.

As explained in the Data section, fish prices were only available by fishing year (y), $\pi_{t,s}$ may then be formulated as $\pi_{t,s} = \pi_{y,s}$. ACE prices ($\chi_{q,s}^{\text{ACE}}$) were only available on a quarterly (q) basis. As explained in the Data section, it is uncertain whether the cost of renting ACE, or paying the deemed value, is already included in the fish price (in which case, $\chi_{t,s} = 0$) or not (in which case, $\chi_{t,s} > 0$). Both scenarios were tested. With the second scenario ($\chi_{t,s} > 0$), we also made the assumption that when ACE prices exceeded the annual deemed value ($\chi_{y,s}^{\text{DV}}$), fishers would rather choose to pay the penalty than to rent an ACE. $\chi_{t,s}$ may then be formulated as

$$\chi_{t,s} = \begin{cases} \chi_{q,s}^{\text{ACE}} \text{ if } \chi_{q,s}^{\text{ACE}} < \chi_{y,s}^{\text{DV}} \\ \chi_{y,s}^{\text{DV}} \text{ if } \chi_{q,s}^{\text{ACE}} \geq \chi_{y,s}^{\text{DV}} \end{cases}$$

Risk management

Fishers may have different attitudes towards risk. Some of them, probably the majority, are risk-averse. These fishers will endeavor to minimize the risk of not achieving their expected profit. To the contrary, risk seekers will explore the métiers for which the track records of profit are most uncertain, with the hope of exceeding the expected profit. In this investigation, we assume that the CVs of last month's and last year's VPUE (referred to here as short- and long-term variability, respectively) represent the fishers' risk perception of operating a given métier, and these are integrated into the model structure at the bottom decision level.

Traditions

Fishers may, or may not, operate the métiers for which they have the greatest experience. This can be reflected by an adherence towards either the most recent métier that they have experienced (short-term adherence) or the métier that they have operated in the previous year and during the same season (long-term adherence). For each vessel v, we represent these adherences by the proportion of fishing effort allocated by that vessel to each métier (i) during the month preceding its fishing trip (short-term adherence) and (*ii*) one year before its fishing trip (long-term adherence). Traditions may have an influence a priori on the choice of gears and management units, as well as on target species and statistical areas. We define the short-term adherence at the bottom decision level (targeting index choice) and the top decision level (gear and management unit choice) as ADH1_1 and ADH2_1, respectively. Similarly, we define the long-term adherence at the bottom and at the top decision levels as ADH1_12 and ADH2_12, respectively. The adherence variables may be formulated as

$$\text{ADH1_1}_{v,m} = \text{ADH1}_{t-1,v,m} = \frac{\sum_{i \in N_{v,m}} [E_{t-1,v,i}]}{\sum_{m \in C_{g,u}} \sum_{i \in N_m} [E_{t-1,v,i}]}$$

$$\text{ADH2_1}_{v,g,u} = \text{ADH2}_{t-1,v,g,u} = \frac{\sum_{i \in N_{v,u}} [E_{t-1,v,i}]}{\sum_{g,u \in C} \sum_{i \in N_{v,u}} [E_{t-1,v,i}]}$$

$$\text{ADH1_12}_{v,m} = \text{ADH1}_{t-12,v,m} = \frac{\sum_{i \in N_m} [E_{t-12,v,i}]}{\sum_{m \in C_{g,u}} \sum_{i \in N_m} [E_{t-12,v,i}]}$$

$$\text{ADH2_12}_{v,g,u} = \text{ADH2}_{t-12,v,g,u} = \frac{\sum_{i \in N_{v,u}} [E_{t-12,v,i}]}{\sum_{g,u \in C} \sum_{i \in N_{v,u}} [E_{t-12,v,i}]}$$

where $C_{g,u}$ is the subset of métiers operated with gear g and in management unit u, and C is the set of possible combinations of gears and management units.

Catch plans and penalty functions

Maximizing expected profit does not necessarily guarantee the best economic return for fishers operating mixed fisheries. This is particularly true for the New Zealand ITQ fisheries. For instance, in New Zealand, the quota owners may not necessarily be fishers. As a result, a number of fishers have contractual arrangements with quota holding companies. In return, fishers are contracted to land a pre-agreed species composition. Fulfilling the contract does not necessarily provide the best economic return that fishers could expect from a fishing trip, but it gives them an access to ACE and a channel to sell their fish at an appropriate price. To the contrary, if fishers' catch composition is too different from that contracted, they may pay a high deemed value and may even not be in a position to sell fish they landed in excess, while they may not be in a position to honor their contract when landing an insufficient amount of other fish.

In this study, we developed penalty functions that measure the difference, averaged over all stocks, between the catch plan owned by fishers before they start a fishing trip and the catch composition they expect from that trip when operating a given métier. A catch plan (Z_s) is here defined for any stock $s \in N_S$ as the proportion of the catch weight planned for stock s relative to the total catch weight planned for all stocks included in the catch plan. Similar to the approach followed to estimate the expected profit, we assumed here that the skipper of each individual vessel v operating fishing trip i could in principle estimate the expected catch composition when choosing a given métier based on the 1- and 12-month lag yields averaged over all vessels belonging to the same fleet and all fishing trips belonging to the same métier.

Catch plans are defined by stock, which themselves consist of a combination of species and management units. Catch plans could therefore determine the choice of gears and management units at the top decision level. Because stock densities are subject to important spatial variations, we assumed that yields in both the previous month and the previous year could influence métier choices at the bottom decision level. Overall, the penalty functions may then potentially influence métier choice at both top and bottom decision levels. We therefore define four penalty functions variables to represent the short-term consistency between catch plans and expected catch compositions at both bottom and top decision levels (PEN1_1 and PEN2_1, respectively) and the long-term consistency for each of these levels (PEN1_12 and PEN2_12, respectively). The penalty functions may be formulated as

$$\text{PEN1_1}_{f,m} = \text{PEN1}_{t-1,f,m} = \frac{1}{N_S N_f N_m} \sum_{s \in N_S} \sum_{v \in N_f} \sum_{i \in N_m} \left[\frac{Y_{t-1,s,v,i}}{\sum_{s \in N_S} Y_{t-1,s,v,i}} - Z_{s,s,v,i} \right]^2$$

$$\text{PEN2_1}_{f,g,u} = \text{PEN2}_{t-1,f,g,u} = \frac{1}{N_S N_f N_{g,u}} \sum_{s \in N_S} \sum_{v \in N_f} \sum_{i \in N_{v,u}} \left[\frac{Y_{t-1,s,v,i}}{\sum_{s \in N_S} Y_{t-1,s,v,i}} - Z_{s,s,v,i} \right]^2$$

$$\text{PEN1_12}_{f,m} = \text{PEN1}_{t-12,f,m} = \frac{1}{N_S N_f N_m} \sum_{s \in N_S} \sum_{v \in N_f} \sum_{i \in N_m} \left[\frac{Y_{t-12,s,v,i}}{\sum_{s \in N_S} Y_{t-12,s,v,i}} - Z_{s,s,v,i} \right]^2$$

$$\text{PEN2_12}_{f,g,u} = \text{PEN2}_{t-12,f,g,u} = \frac{1}{N_S N_f N_{g,u}} \sum_{s \in N_S} \sum_{v \in N_f} \sum_{i \in N_{v,u}} \left[\frac{Y_{t-12,s,v,i}}{\sum_{s \in N_S} Y_{t-12,s,v,i}} - Z_{s,s,v,i} \right]^2$$

Low values of these penalty functions indicate a high degree

Table 2. Proportion of métiers for which the different short-term (lag 1 month) and long-term (lag 12 months) explanatory variables could not be calculated because of missing values.

Métier type	Fleet	No. of observations	Missing values in explanatory variables (%)	
			Short-term variables	Long-term variables
1	1	16 602	25	23
	2	63 365	27	29
	3	20 285	30	32
	4	36 590	11	12
	5	19 348	26	26
2	1	22 136	33	31
	2	114 057	6	7
	3	28 399	12	12
	4	29 272	11	13
	5	22 112	17	18

of consistency between catch composition and catch plans and vice versa. Because Z is by construction common to the short-term and the long-term penalty functions, there is an element of redundancy between these variables. This was confirmed by preliminary runs of the RUM, which indicated a high correlation between the coefficients associated with short-term and long-term penalty functions. We therefore retained in almost all subsequent analyses only the two short-term penalty functions. However, the long-term penalty functions were used in the 1-year-ahead predictions, where short-term variables could not be included.

Discussions with representatives of some of the major quota holding companies in New Zealand suggested that catch plans are defined annually, before the start of the fishing year, and may be subject to intraannual adjustments during the fishing year. Based on this information, we have formulated the catch plans (Z) as a φ-weighed linear combination of a strategic (or annual) catch plan (SCP) and of a tactical (or adjusted) catch plan (TCP):

$$Z_{s,s,s,f} = (1 - \varphi)\mathrm{SCP}_{s,s,f} + \varphi\mathrm{TCP}_{s,s,s,f}$$

Both the strategic and the tactical catch plans are defined as a proportion of the catch planned for a certain stock relative to the total catch planned for all stocks included in the same catch plan. Although the strategic catch plan is identical for all vessels belonging to fleet f, the tactical catch plan may vary from one vessel to another.

All companies interviewed indicated that strategic catch plans were subject to little interannual changes over the fishing years 2002–2006. In addition, some of the companies provided information from which relative expected catches were extrapolated (see Data section). However, we did not have the elements to fully test how closely the extrapolated relative expected catches were to the actual strategic catch plans. Two alternative approaches, building on different assumptions, have then been pursued to derive strategic catch plans.

First, we considered that the extrapolated relative expected catches could not be used as a reasonable proxy of the actual strategic catch plans. Based on the indication that strategic catch plans were subject to little interannual changes, we then assumed that the strategic catch plan of each fleet could be approached by the average catch composition achieved by that fleet in the previous year and in the same month. The strategic catch plans derived from this assumption are referred to as A-type strategic catch plans (SCP_A) and may be formulated as

$$\mathrm{SCP_A}_{s,s,f} = \frac{Y_{t-12,s,f}}{\sum_{s \in S_f} Y_{t-12,s,f}}$$

Second, we considered that the extrapolated relative expected catches could be used as a reasonable proxy of the actual strategic catch plans. We then derived a B-type strategic catch plan building on these relative expected catches. As explained earlier, the relative expected catch (REC) data were available on a monthly basis for fleets 2–5, but not seasonally for fleet 1. By contrast, relative expected catches were available monthly, but in only one year (2007), for fleets 2–5. Two approaches have then been pursued: one for fleet 1 and one for fleets 2–5.

Table 3. Results from the first preliminary analysis.

		Catch plan option																	
		A-type strategic catch plan									B-type strategic catch plan								
Métier type	Fleet	A1	A2	A3	A4	A5	A6	A7	A8	A9	B1	B2	B3	B4	B5	B6	B7	B8	B9
1	1	0.24	0.21	0.14	0.14	0.12	0.12	**0.26**	0.25	0.18	0.18	0.18	0.10	0.08	0.10	0.12	0.22	0.20	0.17
	2	0.42	0.42	0.42	0.41	0.43	0.42	0.41	0.41	0.43	0.43	0.42	0.42	**0.44**	0.43	0.42	0.43	0.40	0.40
	3	0.37	**0.39**	0.39	0.36	0.34	0.33	0.32	0.34	0.35	0.37	0.37	0.39	0.36	0.33	0.33	0.32	0.33	0.34
	4	0.15	**0.16**	0.15	0.15	0.15	0.14	0.15	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14
	5	**0.26**	0.24	0.23	0.24	0.22	0.22	0.24	0.24	0.23	0.21	0.21	0.21	0.21	0.22	0.22	0.22	0.22	0.22
2	1	0.31	**0.31**	0.27	0.25	0.25	0.23	0.31	0.27	0.24	0.24	0.25	0.26	0.23	0.24	0.23	0.29	0.27	0.25
	2	0.11	0.11	0.11	0.09	0.09	0.08	0.11	0.10	0.08	0.11	0.10	0.09	0.09	0.08	0.08	**0.11**	0.11	0.09
	3	0.18	0.18	0.19	0.19	0.18	0.19	0.18	0.17	0.17	0.18	0.17	0.18	**0.19**	0.19	0.19	0.19	0.18	0.18
	4	0.14	0.13	0.12	0.12	0.10	0.11	0.13	0.12	0.10	**0.15**	0.12	0.11	0.12	0.11	0.11	0.14	0.13	0.11
	5	0.21	**0.22**	0.20	0.20	0.20	0.19	0.21	0.21	0.20	0.21	0.20	0.20	0.20	0.20	0.19	0.21	0.21	0.20

Note: Proportion of correct-choice predictions obtained with the different penalty functions calculated with the assumption that the catch plan is a linear combination of the current relative ACE availability and either the previous year's catch proportion by stock (A-type strategic catch plan) or a monthly catch proportion by stock estimated based on industry data (B-type strategic catch plan). For each run, the only explanatory variables are the two short-term penalty functions. The highest proportion for each category is indicated in bold type.

Table 4. Second preliminary analysis.

Fleet	Métier typology	Catch plan option	Run no. 1	2	3	4	5
1	1	A7	0.56	0.14	*	*	0.60
	2	A2	0.48	0.21	*	*	0.53
2	1	B4	0.79	0.32	*	*	0.81
	2	B7	0.74	0.04	0.05	0.05	0.74
3	1	A2	0.64	0.25	*	*	0.67
	2	B4	0.56	0.07	0.08	0.08	0.57
4	1	A2	0.33	0.04	0.06	0.06	0.34
	2	B1	0.38	0.05	0.06	0.07	0.40
5	1	A1	0.62	0.14	0.17	0.17	0.64
	2	A2	0.60	0.07	0.09	0.10	0.60

Note: McFadden's likelihood ratio index statistic obtained with different parameterization of the RUM corresponding to runs 1–5. An asterisk (*) indicates that the McFadden's likelihood ratio index statistic could not be computed. The cost of renting ACE, or paying the deemed value, has been deducted from the available fish price.

For fleets 2–5, the B-type strategic catch plan (SCP_B) was then simply derived as

$$\text{SCP_B}_{s,s,f} = \text{REC}_{s,s,f}$$

For fleet 1, we introduced a seasonal component into the strategic catch plan by combining relative expected catches with the seasonal distribution of each species catch in the previous year. If y represents the fishing year, the B-type strategic catch plan was then formulated for fleet 1 as

$$\text{SCP_B}_{s,s,f} = \text{REC}_{s,s,f}\left(\frac{Y_{t-12,s,f}}{\sum_{t\in y-1} Y_{t,s,f}}\right)$$

To estimate the tactical catch plan, we made the assumption that the various intraannual adjustments that operated on the strategic catch plan were directly linked to the current ACE availability. The tactical catch plan was then modeled as

$$\text{TCP}_{t,s,s,f} = \frac{\max\left[0, \text{ACE}_{q,s,s,f} - \sum_{\tau\le t} Y_{\tau,s,s,f}\right]}{\sum_{s\in N_s}\left(\max\left[0, \text{ACE}_{q,s,s,f} - \sum_{\tau\le t} Y_{\tau,s,s,f}\right]\right)}$$

The parameter φ balances the strategic and the tactical catch plans and is constructed to be in the range [0, 1]. When φ = 0, the strategic catch plan is never adjusted throughout the year. When φ = 1, fishers do not follow any specific annual strategy, and the catch plan is entirely driven by ACE availability. Different values of φ were tested in this investigation. First, we varied φ between 0 and 1 (by step increments of 1/5) irrespective of when the fishing trip happened in the fishing year. Second, because ACE availability is generally more constraining at the end than at the start of a fishing year, we explored the possibilities of having catch plans driven entirely by (*i*) the strategic catch plan in the first quarter(s) of the fishing year (φ = 0) and (*ii*) the tactical catch plan in the last quarter(s) of the fishing year (φ = 1). Eighteen catch plan options have been investigated. Options A1–A9 build on A-type strategic catch plans, whereas options B1–B9 are derived from B-type strategic catch plans. The first six options within each strategic catch plan category (A1–A6 or B1–B6) assign values to φ of 0.0, 0.2, 0.4, 0.6, 0.8, and 1.0. Note that options A6 and B6, which assume that fishers do not follow a specific annual strategy, are equivalent. Options A7 and B7 assume that the strategic catch plan is followed in the first three quarters of the fishing year and the tactical catch plan in the last quarter. Options A8 and B8 assume that the strategic catch plan is followed in the first two quarters of the fishing year and the tactical catch plan in the last two quarters. Finally, options A9 and B9 assume that the strategic catch plan is followed in the first quarter of the fishing year and the tactical catch plan in the last three quarters.

Missing values

In some occasions, the short-term and long-term VPUE, variability, and penalty functions could not be derived for a number of métiers because no trips were operating these métiers over the period when these variables were calculated. Six percent to 33% of the observations included missing values (Table 2). Removing these observations would be too costly. To fill in the missing observations, we made the assumption that the underlying reason for not operating a métier was that this métier was unattractive. Therefore, we replaced the missing values occurring in the explanatory variables by an unrealistically high value ($+1.0 \times 10^3$ in the case of short-term and long-term variability and penalty functions) or an unrealistically low value (-1.0×10^3 in the case of short-term and long-term VPUE). We also evaluated the sensitivity of the results with respect to the choice of the imputed value by replacing the missing values with the maximum (variability and penalty functions) or the minimum (VPUE) observed for each fleet. This alternative replacement procedure aims at allowing the model to retain, in principle, some low probability of choosing the unattractive métiers.

Model parameterization

To parameterize the final run of the RUM, we carried out

Table 5. Detailed results of run 5.

			Explanatory variables and McFadden's LRI						
Fleet	Catch plan	Métier typology	AD#2_1	AD#2_12	AD#1_1	AD#1_12	PEN2_1	PEN1_1	VPUE_1
1	A7	1	0.0080*	0.0050	0.0377**	0.0437**	–0.0008*	0.0001	0.0001*
	A2	2	0.0081**	0.0092**	0.0204**	0.0170**	–0.0007**	–0.0006*	0.0001**
2	B4	1	0.0096**	0.0092**	0.0244**	0.0155**	0.0014*	–0.0019**	0.0000
	B7	2	0.0153**	0.0136**	0.0327**	0.0180**	–0.0005	–0.0007*	0.0002*
3	A2	1	0.0108**	0.0106**	0.0236**	0.0120**	–0.0008*	–0.0007*	0.0004*
	B4	2	0.0033	0.0095*	0.0301**	0.0102**	–0.0006*	–0.0005*	–0.0000
4	A2	1	0.0120**	0.0081**	0.0273**	0.0121**	–0.0004*	–0.0005*	0.0000
	B1	2	0.0013	0.0010	0.0272**	0.0148**	0.0010*	–0.0018**	–0.0000
5	A1	1	0.0232**	0.0149**	0.0232**	0.0100**	0.0002	–0.0006*	0.0002*
	A2	2	0.0146**	0.0000	0.0239**	0.0162**	–0.0004*	0.0004*	0.0001*

Note: Parameters estimated by the nested logit RUM; *, $p < 0.05$; **, $p < 0.0001$. IV1–IV5 are the inclusive value parameters associated with the different respectively, at the top level of the decision tree; AD#1_1 and AD#1_12, short- and long-term adherences, respectively, at the bottom level of the function at the bottom level of the decision tree; VPUE_1 and VPUE_12, short- and long-term VPUE, respectively, at the bottom level of the decision tree inclusive values. LRI is the McFadden's likelihood ratio index. The cost of renting ACE, or paying the deemed value, has been deducted from the

three preliminary analyses using the complete data set (fishing years 2002–2006). The first preliminary analysis was dedicated to the identification of the most appropriate catch plan. Different catch plan options were tested, using the short-term penalty functions as explanatory variables. For each catch plan, fleet, and typology, we derived the proportion of correct métier predictions as the number of trips for which the model correctly predicted the métier actually chosen relative to the total number of trips in the data set. The catch plan resulting in the largest proportion of correct métier predictions was then selected for future analyses.

The second preliminary analysis investigated the relative weight of the different explanatory variables in the model's goodness of fit, as reflected by McFadden's likelihood ratio index, which is analogous to the R^2 in a classical linear regression model (McFadden 1974). Five runs were carried out with different combinations of the explanatory variables. Run 1 includes short- and long-term adherence to traditions at both decision levels. Run 2 includes only the penalty functions. Run 3 includes the VPUE and their CV at the top decision level and the short-term penalty at the bottom decision level. Run 4 is similar to run 3 but also includes the short-term penalty at the top decision level. Run 5 included all the explanatory variables together with the exception of the lag 12 month penalty functions, which, to a large extent, are redundant with the lag 1 month penalty functions, as explained above. Runs 3–5 were carried out separately with the two assumptions on fish prices (the cost of renting ACE, or paying the deemed value, is or is not already included in the fish price).

Model predictions

We evaluated the capacity of the parameterized model to predict future effort allocation by month and by métier based on a selection of explanatory variables. The model estimation was then based on the data covering only fishing years 2002–2005 (i.e., from 1 October 2001 to 30 September 2005), and the predictions were made for the fishing year 2006 (i.e., from 1 October 2005 to 30 September 2006). We investigated two types of predictions.

First, we evaluated the capacity of the model to make predictions one month ahead. The explanatory variables selected to that purpose were those of run 5, i.e., the short- and long-term adherences, VPUE, variability, and the short-term penalty functions.

Second, we evaluated the capacity of the model to make predictions one year ahead, and only the long-term adherences, VPUE, variability, and penalty functions were selected.

Results

The results of the first preliminary analysis are provided (Table 3). The proportion of correct predictions was dependent on the catch plan option. The proportion of correct predictions was always lower than 50%, suggesting that variables other than penalty functions have an influence on fishers' decision-making. These have been investigated in subsequent runs of the model.

Consider métier type 1. In the case of fleets 3–5, the most suitable catch plan (i.e., that leading to the greatest proportion of correct predictions) appeared to be entirely ($\varphi = 0.0$) or mainly ($\varphi = 0.2$) driven by the strategic plan set at the start of the fishing season. In the case of fleet 2, the most suitable catch plan appeared to be mainly ($\varphi = 0.6$) driven by ACE availability. In the case of fleet 1, fishers appeared to base their catch plan on their initial strategic catch plan for the first three quarters of the fishing year, only to adjust it to prevailing ACE availability during the last quarter. Except for fleet 2, the most suitable catch plans were those calculated using the previous year's catch composition.

Consider métier type 2. For fleets 1, 4, and 5, the most suitable catch plan appeared to be entirely ($\varphi = 0.0$) or mainly ($\varphi = 0.2$) driven by the strategic plan. In the case of fleet 2, fishers appeared to base their catch plan on their initial strategic catch plan for the first three quarters of the fishing year, only to adjust it to prevailing ACE availability during the last quarter. In the case of fleet 3, the most suitable catch plan appeared to be mainly ($\varphi = 0.6$) driven by ACE availability. In the case of fleet 3, effort allocation does not seem to be affected by catch plans, irrespective of the option retained. The most suitable catch plans were those calculated using the previous year's catch composition

CV_1	VPUE_12	CV_12	IV1	IV2	IV3	IV4	IV5	LRI
–0.0001	0.0002*	–0.0017**	0.38**	0.33**	0.22*	0.32**	0.21*	0.60
–0.0002	0.0001**	–0.0006**	0.75**	0.70**	0.60**	0.70**	0.48**	0.53
–0.0011**	0.0000	–0.0006**	0.61**	0.57**	1.11**	—	—	0.81
–0.0007*	0.0004**	–0.0005*	0.37**	0.33**	0.71**	—	—	0.74
–0.0005	–0.0002	–0.0013**	0.46*	0.57**	0.08	—	—	0.67
–0.0001	–0.0003	–0.0007**	0.75**	0.89**	0.48**	—	—	0.57
–0.0004*	0.0003**	–0.0001	0.42**	0.35**	0.26*	—	—	0.34
0.0002	0.0001*	–0.0003*	0.88**	0.89**	0.79**	—	—	0.40
–0.0001	0.0001	–0.0006*	0.11	0.13	0.52*	—	—	0.64
–0.0006*	0.0001**	0.0000	0.72**	0.90**	1.35**	—	—	0.60

level 2 métiers presented in Table 1. The explanatory variables: AD#2_1 and AD#2_12, short- and long-term adherences, decision tree; PEN2_1, short-term penalty function at the top level of the decision tree; PEN1_1, short-term penalty CV_1 and CV_12, short- and long-term variability, respectively, at the bottom level of the decision tree; IV1–IV5, available fish price.

(fleets 1 and 5) or those extrapolated from actual data (fleets 2–4).

The results of the second preliminary analysis, carried out with the most appropriate catch plans (as identified in Table 3) and assuming that the cost of renting ACE, or paying the deemed value, had to be deducted from the available fish price, are presented in Tables 4 and 5. The alternative assumption (costs already including in fish price) was tested and never led to an improvement of the model's goodness of fit for any of the runs and was not considered in subsequent analyses.

The adherence (or tradition) variables contribute the most to the model's explained variability for all fleets and métier typologies (33%–79%) (Table 4). The penalty functions alone also explain a substantial amount of the model's variability (4%–32%). Combining the economic variables with the penalty functions did not result in a substantial increase in the McFadden's likelihood ratio index. With all variables included, the McFadden's likelihood ratio index was reasonably high, above 34% for all fleets and métier typologies and above 50% for all fleets except 4 (Table 4). In a few cases (all with intermediary runs 3 and 4), the McFadden's likelihood ratio index statistic could not be computed, as one of the inclusive values was constrained to zero. This result indicates that on these particular occasions, the decision tree built to reflect fishers' decision-making, combined with the model formulation of runs 3 and 4, did not provide useful fits to the data.

In the outcomes of run 5, almost all coefficients associated with the adherence variables are highly significant ($p < 0.0001$) for all of the combinations of fleets and métier typologies (Table 5). These results indicate that fishers' behavior is generally strongly influenced by the way in which they traditionally allocate their fishing effort, irrespective of the prevailing conditions.

For all combinations of fleets and métier typologies, at least one of the two coefficients associated with the short-term penalty functions was significant ($p < 0.05$ and (or) $p < 0.0001$) and took a negative value. In five out of 10 combinations, both coefficients were significantly lower than zero. Significantly positive values for such coefficients occurred for three combinations and were due to colinearity between the coefficients associated with the two short-term penalty functions. For all combinations of fleets and métier typologies, at least one of the two coefficients associated with the expected VPUE was significantly greater than zero, whereas at least one of the two coefficients associated with variability was significantly lower than zero. In almost all cases, the inclusive values are in the range [0, 1], suggesting that the nested logit was a correct approach to structuring the RUM. In only two cases, the inclusive values were greater than 1 (IV3 = 1.11 for fleet 2 and métier typology 1; IV3 = 1.35 for fleet 5 and métier typology 2).

We also operated the final run by replacing missing values by the maxima (variability and penalty functions) or minima (VPUEs) observed for each fleet. The outcomes were similar to the base case. In particular, the McFadden's likelihood ratio index never differed by more than 1% compared with the base case for any combination of fleets and métier types.

The performance of our model is illustrated with respect to both the calibration to the data of fishing years 2002–2005 (i.e., from 1 October 2001 to 30 September 2005) and the capacity to predict future effort allocation in fishing year 2006 (i.e., from 1 October 2005 to 30 September 2006) using the past data (Tables 6*a*–6*b*; Figs. 4 and 5). The calibration of the RUM to fishing years 2002–2006 data is reasonably good for the main métiers operated by the fleets under investigations. The percentage of correct métier allocation was above 50% for 23 of the 30 combinations of fleets and métiers defined by typology 1 and for 29 of the 40 combinations of fleets and métiers defined by typology 2. Only the least represented métiers were not so well predicted. In most of the combinations of fleets and métier typologies, our model could predict reasonably well future effort allocations one month and even one year ahead for all fleets except the snapper trawlers and for the most important operated métiers (e.g., Figs. 4*a*–4*c*, 4*e*, and 5*a*–5*c*). There were cases, however, in which good calibration and good predictions 1 month ahead did not necessarily result in good predictions 12 months ahead (e.g., Fig. 5*e*). The fit was generally poor for the snapper trawlers, although the

Table 6. Proportion of correct métier choices (p) as calibrated by the RUM using (*a*) métier typology 1 and (*b*) métier typology 2, over fishing years 2002–2005 (i.e., from 1 October 2001 to 30 September 2005) and predicted in the fishing year 2006 (with the 2002–2005 data used to calibrate the model).

(*a*) Typology 1.

	Métier			Calibration		Prediction		
Fleet	Gear	Management unit	Target species	N	p	N	p (1 month)	p (12 months)
1	Bottom trawl	3	Hoki	105	0.52	20	0.40	0.30
			Other species	655	0.91	246	0.85	0.76
		7	All species	423	0.74	61	0.66	0.57
	Midwater trawl	2	All species	97	0.57	40	0.13	0.10
		7	Hoki	700	0.85	165	0.76	0.87
	Other gears and MU		All species	162	0.53	93	0.48	0.11
2	Bottom longline	1A	Snapper	6122	0.93	1387	0.94	0.87
			Other species	139	0.39	17	0.00	0.35
		1B	Snapper	4053	0.91	813	0.94	0.86
			Other species	22	0.95	0	—	—
	Other gears and MU		All species	45	0.82	75	0.33	0.00
3	Bottom longline	1A	Snapper	1847	0.82	528	0.87	0.70
			Other species	27	0.37	34	0.29	0.21
		1B	Snapper	1106	0.86	379	0.84	0.66
	Other gears and MU		All species	106	0.35	30	0.10	0.00
4	Bottom trawl	1A	Gurnard	110	0.48	99	0.79	0.23
			John Dory	269	0.54	80	0.35	0.39
			Snapper	480	0.60	176	0.60	0.53
			Tarakihi	390	0.39	186	0.51	0.27
			Trevally	395	0.54	96	0.71	0.61
			Other species	106	0.25	9	0.00	0.44
		1B	Gurnard	60	0.43	29	0.62	0.14
			John Dory	234	0.52	55	0.45	0.31
			Snapper	185	0.52	126	0.35	0.33
	Other gears and MU		All species	465	0.51	118	0.51	0.60
5	Danish seine	1A	Gurnard	195	0.71	100	0.64	0.46
			Snapper	640	0.82	213	0.83	0.80
			Other species	0	—	14	0.00	0.00
		1B	John Dory	270	0.65	103	0.66	0.35
			Snapper	550	0.80	132	0.80	0.76
			Other species	0	—	10	0.00	0.00
	Other gears and MU		All species	484	0.89	53	0.87	1.00

(*b*) Typology 2.

	Métier			Calibration		Prediction		
Fleet	Gear	Management unit	Statistical area	N	p	N	p (1 month)	p (12 months)
1	Bottom trawl	3	18	99	0.39	26	0.27	0.27
			22	552	0.79	180	0.84	0.65
			Other areas	58	0.64	61	0.21	0.43
		7	All areas	427	0.71	59	0.68	0.64
	Midwater trawl	2	All areas	93	0.46	37	0.11	0.49
		7	17	569	0.75	165	0.76	0.70
			Other areas	129	0.71	0	—	—
	Other gears and MU		Other areas	215	0.49	97	0.48	0.09
2	Bottom longline	1A	2	2407	0.94	640	0.99	0.92
			3	1265	0.81	196	0.69	0.60
			8	1637	0.94	424	0.95	0.86
			9	485	0.91	127	0.87	0.62
			Other areas	510	0.96	16	0.50	0.69
		1B	5	2314	0.81	432	0.86	0.76
			6	616	0.48	133	0.47	0.03
			7	1100	0.78	248	0.85	0.60
	Other gears and MU		All areas	47	0.79	76	0.36	0.00

Table 6 (*concluded*).

(*b*) Typology 2.

	Métier			Calibration		Prediction		
Fleet	Gear	Management unit	Statistical area	*N*	*p*	*N*	*p* (1 month)	*p* (12 months)
3	Bottom longline	1A	2	344	0.56	88	0.69	0.45
			3	1163	0.80	298	0.79	0.61
			8	83	0.55	31	0.32	0.16
			Other areas	272	0.84	144	0.88	0.33
		1B	6	602	0.76	140	0.58	0.58
			Other areas	487	0.77	239	0.74	0.54
	Other gears and MU		All areas	135	0.41	31	0.10	0.00
4	Bottom trawl	1A	3	532	0.77	242	0.74	0.63
			8	178	0.47	124	0.57	0.17
			9	772	0.68	192	0.77	0.67
			10	249	0.41	56	0.52	0.41
			Other areas	24	0.25	35	0.00	0.06
		1B	5	388	0.58	128	0.54	0.45
			Other areas	88	0.20	77	0.29	0.12
	Other gears and MU		All areas	463	0.50	111	0.45	0.39
5	Danish seine	1A	8	276	0.84	89	0.94	0.91
			9	441	0.70	120	0.68	0.48
			10	72	0.24	43	0.33	0.37
			Other areas	57	0.61	68	0.82	0.50
		1B	5	64	0.52	34	0.50	0.18
			6	705	0.81	187	0.79	0.60
			7	83	0.45	30	0.43	0.10
	Other gears and MU		All areas	441	0.93	54	0.59	0.59

Note: Predictions were made 1 month and 12 months ahead. *N* is the number of observations used to calculate *p*.

tendencies were roughly picked up for the main métiers (Figs. 4c and 5c).

Discussion

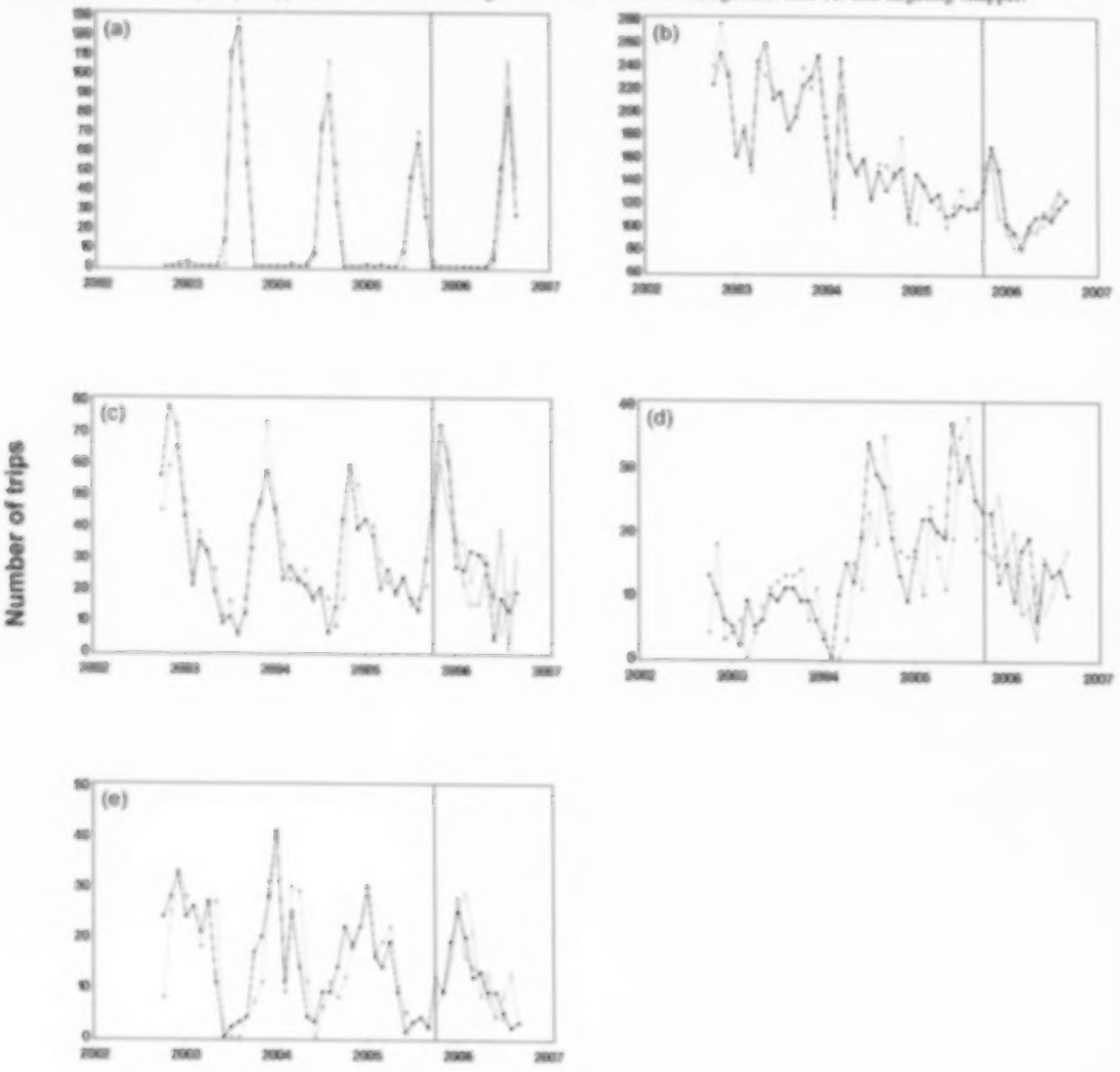
This study bears out that traditions are an important determinant of fishers' behavior. Holland and Sutinen (1999) demonstrated that the tradition variables were by far the most influential determinants of effort allocation for New England trawlers. Pradhan and Leung (2004*a*) showed that Hawaii's longline fishers exhibited a strong adherence to previously operated métiers. However, it remains to be evaluated which factors are actually incorporated into the traditional variables and which are the most influential on fishers' behavior. Traditions surely incorporate habits, but probably also the fishers' experience of how to fish on appropriate fish aggregations. When fishers have a catch plan, appropriate fish aggregations are not only characterized by a high density of fish, but also by the mix of species required by that plan. Eventually, traditions incorporate the fishers' ability to fish in a profitable way and may overlap to some extent with the other variables examined in this study (VPUE, catch plans). This probably explains why the traditional variables appeared as the most determinant factors of fishers' behavior for all the fleets investigated in this study.

A common assumption made is that fishers' behavior is determined by economics. The results of our investigations do not contradict this assumption. However, although a number of studies indicate that averaged past revenues are a determinant of métier choices (Holland and Sutinen 1999; Hutton et al. 2004), our analyses showed that the catch plans allocated to fishers are also influential in the case of the New Zealand fleets being investigated, irrespective of the métier typology used.

To our knowledge, catch plans have never been explicitly integrated as explanatory variables in previous models of fishers' behavior. The reason why catch plans are a determinant of fishers' behavior may be directly linked to the nature of the New Zealand QMS. In ITQ fisheries, ACEs are allocated to fishers, either in the form of contracts with quota holding companies or simply because fishers are themselves quota holders. It is therefore conceivable that matching catch species composition with catch plans is a realistic economic objective for New Zealand fishers. However, and as confirmed with discussions with industry representatives, such an objective is not necessarily consistent with the classical multispecies profit maximization goal at the scale of the fishing trip.

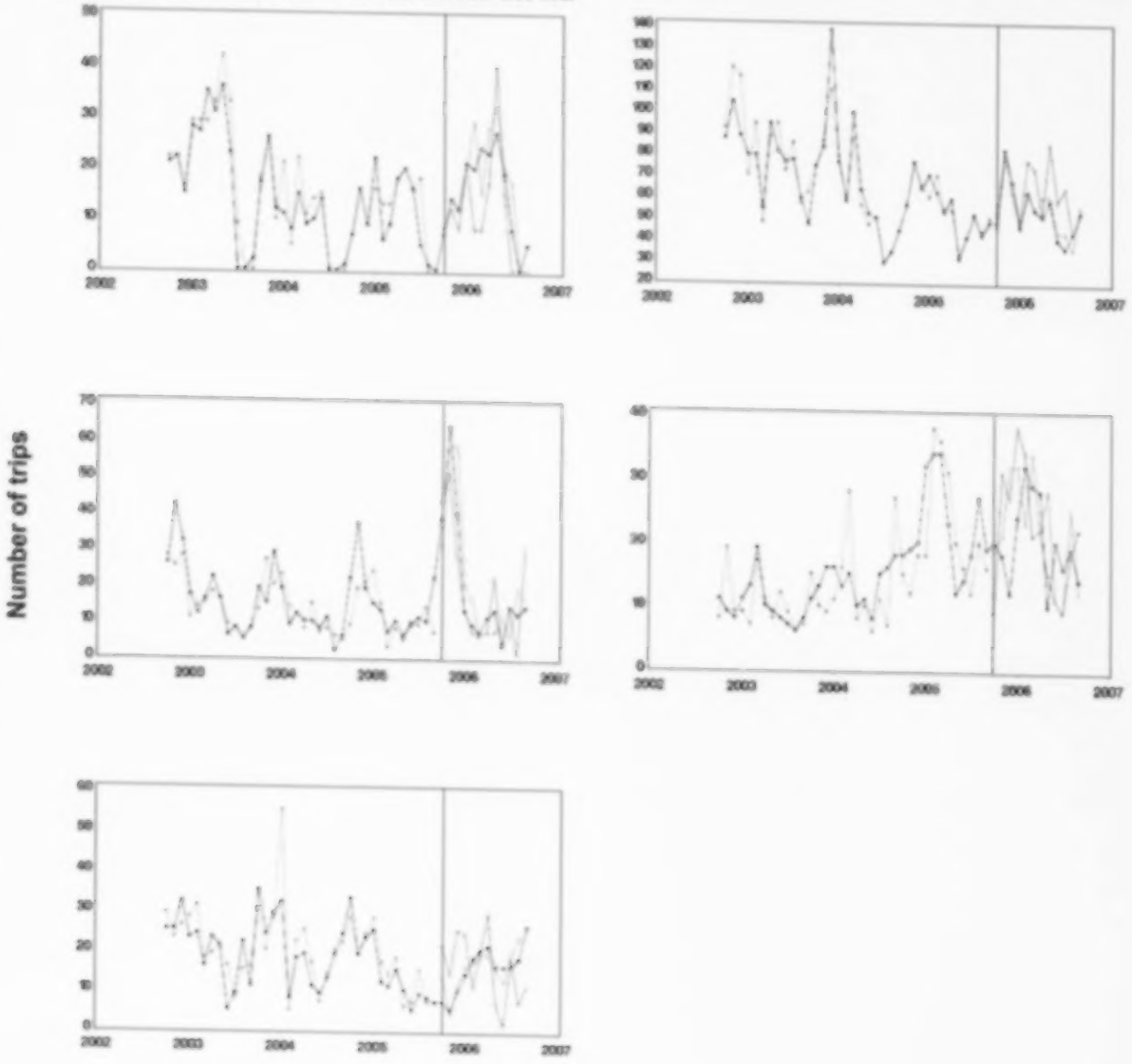
Catch plans were constructed here as an estimated combination of an annual strategy and an intraannual adjustment to prevailing ACE availability. Overall, the catch plans appeared to be determined to a large extent by the annual strategy and subject to little adjustments throughout the fishing year for most fleets and métier types (hoki trawlers, northern snapper trawlers, and seiners for all typologies, small northern snapper longliners with métier based on statistical areas, medium northern snapper longliners with métier based on target species). Interpreting the nature of catch plans should be done cautiously, as they were calculated subject to assumptions. However, there are plausible reasons

Fig. 4. Number of trips observed (solid line, blue dots), calibrated over fishing years 2002–2005 (dotted line, red dots) and predicted over fishing year 2006 (one month ahead, dotted line, green circles; one year ahead, dotted line, black circles). Number of trips per year and per month for each fleet operating its main métier (typology 1): (*a*) fleet 1 fishing with midwater trawls in management unit 7 and targeting hoki (*Macruronus novaezelandiae*); (*b*) fleet 2 fishing with bottom longlines in management unit 1A and targeting snapper (*Pagrus auratus*); (*c*) fleet 3 fishing with bottom longlines in management unit 1B and targeting snapper; (*d*) fleet 4 fishing with bottom trawls in management unit 1A and targeting snapper; and (*e*) fleet 5 fishing with Danish seines in management unit 1B and targeting snapper.



as to why catch plans are mainly influenced by an annual strategy. First, it may be hypothesized that fishers are generally able to follow their strategic catch plan most of the year. When they cannot adhere to the annual plan in a given month, they do not systematically seek for an adjustment in the following months and may well exceed their available ACE. This could be explained by the fact that in New Zealand, the balance between catch and ACE is only evaluated at the end of the fishing year. Therefore, fishers could operate with an insufficient provision of (or even without) ACE during most of the fishing year and then balance their catches, or possibly pay the deemed value, at the end of the

Fig. 5. Number of trips observed (solid line, blue dots), calibrated over fishing years 2002–2005 (dotted line, red dots) and predicted over fishing year 2006 (one month ahead, dotted line, green circles; one year ahead, dotted line, black circles). Number of trips per year and per month for each fleet operating its main métier (typology 2): (*a*) fleet 1 fishing with bottom trawls in management unit 3 and statistical area 022; (*b*) fleet 2 fishing with bottom longlines in management unit 1A and statistical area 002; (*c*) fleet 3 fishing with bottom longlines in all statistical areas of management unit 1B; (*d*) fleet 4 fishing with bottom trawls in management unit 1A and statistical area 003; and (*e*) fleet 5 using Danish seines in management unit 1B and statistical area 006.



fishing year. In the cases of hoki bottom trawlers (with métiers defined based on target species) and small snapper longliners (with métiers defined based on statistical areas), the catch plans appeared to consist of following the annual strategy in the first three quarters of the fishing year and then balancing catches with available ACE in the last quarter. We did not have tangible data to determine why the catch plans of northern snapper small longliners (with métiers defined based on target species) and medium longliners (with métiers defined based on statistical areas) were more subject to intraannual adjustments than for the other combinations of fleets and métier types.

Generally, and except for some of the least represented métiers, the model developed in this study fitted the data

reasonably and was also able to predict, in most cases, future effort allocation both one month and one year ahead. These results could be used to inform management. Typically, catch options recommended by scientists to managers are based on the predicted response of stock biomass to different exploitation rate regimes. A common practice is to estimate the catchability in the prediction year using the historical value derived from the stock assessment. If effort allocation changes in the prediction year (in response to, e.g., substantial shifts in TACs), the assumption of constant catchability could be at fault. The effort allocation model developed in this study could then be used to predict the short-term métier allocation of fishing effort and thereby to refine the derivation of catchability.

This study had a number of limitations. First, some observations had missing values when some métiers were not operated over the period for which explanatory variables were calculated. There is no easy way to resolve this problem. We have first reduced the number of missing values by regrouping rare métiers into more generic categories. Applying this initial prefilter decreased the number of missing observations to 6%–33%, depending on the fleet and métier typology used. To fill in the remaining gaps, we then assumed that métiers were not operated because they were unattractive with respect to the different explanatory variables included in the model. Although this assumption is probably not unreasonable, fishers may have other reasons than those reflected in the explanatory variables of our model for not operating specific métiers. These reasons could include, in particular, great operating costs, recurrently bad weather conditions, or adverse fishing grounds. However, such information was not available to our analysis.

Second, catch plans were calculated subject to a number of assumptions. Two alternative approaches have been considered, one being to extrapolate across vessels and time data collected from the industry, and the other consisting of assuming that catch plans were based on the actual catch compositions from the previous year. We did not have elements to test how close either estimate was to the actual catch plan. We could, however, verify that the catch plans, as estimated using both approaches, were an important determinant of fishers' behavior. With better data coverage, catch plans could be derived more accurately, and their estimated impact on fishers' decision-making might even be greater than suggested in this investigation.

Third, we expressed three concerns with regards to the quality of the fish price information used to derive VPUE. We tested the effect of including or not including the ACE rental in the original fish price and concluded that it hardly affected the results of the analysis. However, we did not explicitly address the other two concerns, i.e., that fish prices were likely underestimated and that seasonal fluctuations in fish prices were not reflected in our annual data set. With more realistic fish price data, VPUE could have been a better profit proxy and might have proved a more influential determinant of fishers' behavior than the current estimate.

Fourth, we did not have the information on whether quotas or vessels were owned by skippers. In fact, it could be important to know whether ACEs are held by individual skippers or by a quota holding company and also whether the skipper is the vessel owner. There is evidence that different types of ownership may result in different strategies and catch plans (Sharma and Leung 1999; Esmaeili 2006).

The succession of decisions made by fishers when electing a métier has here been represented as a two-level process. First, fishers choose a gear and a broad management unit, and second, they refine their choice based on either a target species or a statistical rectangle. This hierarchical structure is a simplification of fishers' decision processes, which was needed to keep the number of métiers tractable for modeling purposes. A third hierarchical level could be contemplated to reflect the decisions that fishers may take in the course of their fishing trip. For instance, fishers may seek specific fish aggregations using echosounders (hoki fishery) or vessel aggregations suggesting high fish densities (Gillis and Showell 2002). To the contrary, fishers may try to avoid competition in congested areas (Gillis and Peterman 1998; Rijnsdorp et al. 2000). Accounting for that third hierarchical level would require refining the time and spatial scale of our métiers, which could be achieved by grouping fishing operations (i.e., tows or sets) instead of fishing trips (Branch et al. 2005).

A logical step forward from this study would be to talk to the skippers themselves to verify the outcomes of our model. This approach could also be pursued to investigate the assumptions that have been made during the modeling process. Other logical follow-ups to our analyses could be to couple our approach with a model of vessels entering and exiting fishing fleets (Pradhan and Leung 2004*b*) and also to integrate the fleet dynamics processes in a comprehensive bio-economic model. This model could be used to make a fuller evaluation of the ITQ system. The scenarios to be investigated could include changes in TACs, ACE allocation rules, and the process of deemed value setting rules.

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Appendix A. Details of the random utility model

In a random utility model, the utility function ($U_{v,i,m}$) associated with vessel v, fishing trip i, and métier m can be decomposed into deterministic ($x'_{v,i,m}\alpha$) and stochastic ($\varepsilon_{v,i,m}$) components:

$$U_{v,i,m} = x'_{v,i,m}\alpha + \varepsilon_{v,i,m}$$

where $x'_{v,i,m}$ is a vector of explanatory variables (to be detailed later) and α is a vector of parameters to be estimated. Different distributions may be contemplated for the stochastic component $\varepsilon_{v,i,m}$, leading to different model types. The simplest forms are the conditional and the multinomial logit models (Hutton et al. 2004). However, a critical aspect of both distribution models is that they should accommodate the property of independence of irrelevant alternatives. This property imposes, in particular, that the different alternatives in the choice set are independent, so a change in that choice set (e.g., by removing one alternative) should not affect parameters estimates. In many cases, this assumption appears to be violated (Wilen et al. 2002) and preliminary RUM runs carried out in this study with a conditional logit model also lead to the same conclusion. Alternative model types have been used in past studies to relax the independence of irrelevant alternatives property in different ways, such as the mixed logit model (Pradhan and Leung 2004) and the nested logit model (Holland and Sutinen 1999).

In principle, both the mixed logit and the nested logit forms could be used here. We decided to apply the nested logit model, as it imposes a hierarchical structure, which conceptually could accommodate the organization of the fishers' decision-making process (Holland and Sutinen 1999).

We specify here a two-level nested logit model. We assume that fishers would select first (at the top decision level) one main gear and a management unit and then choose (at the bottom decision level) a specific target species (métier type 1) or a more precise statistical area (métier type 2). Some explanatory variables belonging to vector x will come into the model at the top decision level (vector of variables z), and others will come in at the bottom decision level (vector of variables y).

With the two-level nested logit model, the unconditional probability $P(v,i,m)$ that vessel v will choose a métier m during fishing trip i may be expressed as

$$P(v,i,m) = P(v,i,g,u) \cdot P(v,i,m|g,u)$$

where $P(v,i,m|g,u)$ is the conditional probability that vessel v will choose, during fishing trip i, a métier m after having selected gear g and management unit u. $P(v,i,g,u)$ is the unconditional probability that vessel v will choose during fishing trip i a gear g and a management unit u. $P(v,i,m|g,u)$ may be expressed as

$$P(v,i,m|g,u) = \frac{\exp\{y_{v,i,m|g,u}\beta\}}{\sum_{m\in C_{g,u}} \exp\{y_{v,i,m|g,u}\beta\}}$$

where β is the vector of parameters to be estimated in relation to y, and $C_{g,u}$ is the subset of métiers operated with gear g and in management unit u. $P(v,i,g,u)$ may be expressed as

$$P(v,i,g,u) = \frac{\exp\{z'_{v,i,g,u}\gamma + \mathrm{IV}_{g,u}\delta_{g,u}\}}{\sum_{g,u\in C} \exp\{z'_{v,i,g,u}\gamma + \mathrm{IV}_{g,u}\delta_{g,u}\}}$$

where C is the set of possible combinations of gears and management units, γ is the vector of parameters to be estimated in relation to z, and the inclusive value (IV) is the average utility that individuals may expect from each combination of gear and management unit. The inclusive value parameters (δ) are estimated by the RUM. Although these parameters should, in principle, be in the range [0, 1] if the nested logit is the correct model specification, Herriges and Kling (1996) demonstrated that values beyond that range could, under certain conditions, be locally consistent with such models. The inclusive values may be formulated as

$$\mathrm{IV}_{g,u} = \ln\left\{\sum_{m\in C_{g,u}} \exp\{y_{v,i,m|g,u}\beta\}\right\}$$

The different parameters of the nested logit model are then estimated using the full information maximum likelihood method.

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Searching for threshold shifts in spawner–recruit data

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Abstract: Relationships between spawning fish (*S*) and surviving offspring (recruits, *R*) are typically assumed to be continuous and nonlinear. However, *R* may change abruptly with small changes in *S* if population-, community-, or ecosystem-scale processes trigger low adult reproduction and cause populations to shift abruptly to regimes of low recruitment. We simulated *R* with low mean and variation below a known *S* threshold and high mean and variation of *R* above it. We compared simulations with published *S*–*R* relationships. For all data, we fit a conventional Ricker-type *S*–*R* model, a logistic depensatory model, and also searched for an *S* breakpoint with a nonparametric test. The Ricker and logistic models often fit discontinuous simulated data. The nonparametric test found the *S* threshold in simulated data, although its accuracy depended on underlying distributions. The Ricker and logistic models and the nonparametric test identified apparent relationships within published data, sharing common results in <50% of the data sets. Although population models often assume continuous relationships, discontinuous threshold changes in *R* with small changes in *S* may occur. Identification of the conditions that reproductive state changes abruptly in fish populations may be necessary to develop risk-averse regulatory policies.

Résumé : On assume généralement que les relations entre les poissons reproducteurs (*S*) et les rejetons survivants (recrues, *R*) sont continues et non linéaires. Cependant, *R* peut changer abruptement à la suite de petites modifications de *S* si les processus qui opèrent à l'échelle de la population, de la communauté ou de l'écosystème déclenchent une reproduction adulte faible et forcent les populations à passer rapidement dans un régime de recrutement faible. Nous avons fait des simulations dans lesquelles *R* possède une moyenne et une variation faibles sous un seuil connu de *S* et une moyenne et variation élevées au-dessus du seuil. Nous avons comparé nos simulations avec des relations *S*–*R* de la littérature. Sur l'ensemble des données, nous avons ajusté un modèle *S*–*R* classique de type Ricker et un modèle logistique à effet Allee et avons recherché un point de rupture de *S* avec un test non paramétrique. Le modèle de Ricker et le modèle logistique s'ajustent souvent aux données simulées discontinues. Le test non paramétrique a trouvé le seuil de *S* dans les données simulées, bien que la précision dépende des distributions sous-jacentes. Le modèle de Ricker, le modèle logistique et le test non paramétrique ont identifié des relations apparentes dans les données publiées, obtenant des résultats communs dans <50 % des ensembles de données. Bien que les modèles démographiques présupposent souvent des relations continues, il peut se produire chez *R* des discontinuités et des seuils à cause de petits changements de *S*. Il peut être nécessaire d'identifier les conditions sous lesquelles l'état reproductif des populations de poissons change abruptement afin de mettre sur pied des politiques de réglementation qui minimisent les risques.

[Traduit par la Rédaction]

Introduction

Understanding how fisheries respond to harvest requires sound information about population dynamics in the face of complex and perhaps counterintuitive underlying processes. Managing these complex systems often involves forecasting the density of fish recruiting to the fishery to set production expectations and derive harvest limits (Ricker 1975). Given that adult fish are typically targeted for harvest, it is important to generate relationships between the density of adult spawners and the number of surviving offspring produced to determine the escapement needed to sustain populations. These relationships often are fitted with continuous functional models (e.g., classic Ricker or Beverton–Holt curves or nonlinear regression models) that depend on assumptions about continuous underlying population mechanisms, such as compensation and depensation.

We suggest that fitting continuous functional models to spawner–recruit relationships may not always be appropriate. Rather, discontinuous processes may be at play, contributing to rapid, possibly threshold shifts in reproductive output as a function of adult density, ultimately leading to regime shifts within fish assemblages (Steele and Henderson 1984; Collie et al. 2004; Schroder et al. 2005). At some region of low spawner densities, low recruit density may occur (Fig. 1; Holling 1973). Above this region, another regime of high but possibly more variable recruitment may exist (Fig. 1). This occurs because the number of offspring

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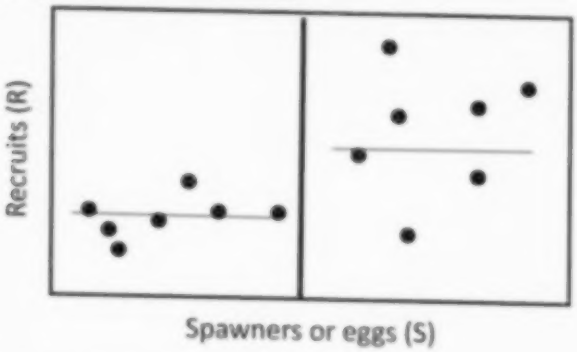
Fig. 1. Conceptual stock–recruitment scenario in which two recruitment regime states occur. Each point is a hypothetical annual sample from a population. The vertical line is the spawner or egg density (S) at which a two-dimensional Kolmogorov–Smirnov (2DKS) test finds the point of greatest difference in recruit production (R). Below some "region" of spawner abundance, the stable, equilibrium, recruit abundance is very low. Above this region, potential average recruitment is high, but stochastic environmental conditions create more variability. The 2DKS will identify the region of spawner densities where expected recruits produced shift between these two regimes. Two horizontal mean lines can be fitted through these data to the left and right of the breakpoint. A logistic or Ricker model also may fit this relationship, although the underlying distribution is discontinuous.



produced is no longer limited by adults and rather is primarily affected by external processes (Leggett and DeBlois 1994; Myers 2002). In other words, ecological release from the limited factor of hatchling production occurs and some other limiting factor (or suite of factors) is at play.

Some populations may have inherent characteristics that make them vulnerable to threshold shifts between low and high recruitment (Fig. 1). Populations may contain phenotypes with unique life histories (e.g., alternative reproductive stable strategies, Gross 1991) that affect reproductive behavior and subsequent recruitment. It is plausible that declining densities of adults may cause rapid changes in the frequency of reproductive phenotypes (e.g., earlier maturation and lower fecundity, Jennings and Philipp 1992) that subsequently result in shifting recruitment regimes (Conover and Munch 2002). In harvested populations, the behavior of fish and their fishers may change abruptly as adults decline (e.g., both may become aggregated, thereby increasing fishing pressure), again causing rapid shifts toward low recruitment (Post et al. 2002). These mechanisms are often considered depensatory because the reproductive output of individual fish declines rather than increases as population density declines.

From a community perspective, it is common for the outcome of predator and prey interactions to depend on life stage (e.g., intraguild interactions, Polis and Holt 1992; Olson et al. 1995). Early life stages of predators and prey may compete, with young prey being superior competitors; adult prey also may consume young predators. If adult predator densities are low and cannot control prey recruitment, then early life stages of prey dominate and suppress predator dominance by reducing predator recruitment (Walters and Kitchell 2001). These types of interactions create stable states of low predator density when adult predator densities decline to some threshold region (Bampfylde and Lewis 2007). A classic example is the bluegill (*Lepomis macrochirus*) crowded state that often occurs in small North American lakes, in which small, dense bluegill populations control recruitment of their primary predator, largemouth bass (*Micropterus salmoides*) (Flickinger et al. 1999).

Ecosystem feedbacks also may cause abrupt shifts in recruitment. Spawning adults may modify their environment in ways that enhance the success of their recruits, such as releasing nutrients from their carcasses after spawning (Naiman et al. 2002). Below some threshold density, adults may no longer provide sufficient environmental conditions to enhance community conditions (i.e., primary and secondary production) that promote survival of their offspring. Again, the result may be a rapid shift to low recruitment. Once the ecosystem has reached a state of low, externally derived subsidies, it may be difficult for it to return to a state of high adult production and increased recruitment without human management (Budy et al. 1998) and ample time for recovery.

We explored whether different recruitment regimes may plausibly exist within fish populations as an alternative to continuous relationships by first simulating expected patterns based on simple assumptions about the production of recruits at spawner densities at which recruitment regime states may change. We treated these spawner densities as threshold random variables ranging from invariant to highly variable, because regimes of recruit production likely vary among years and systems, depending on factors suppressing recruitment at low spawner densities and density-independent factors that affect adult recruitment success at high spawner densities. We then compared these simulated distributions with published spawner–recruit relationships. For both the simulated and actual data sets, we used both continuous models and discontinuous statistical tests (*i*) to determine whether such apparently discontinuous recruit regimes are common and may be mistaken for continuous relationships, (*ii*) to hypothesize about underlying processes, and (*iii*) to assess whether identifying purported spawner thresholds and related recruitment regimes is useful for the management and conservation of fisheries.

Materials and methods

We used computer simulations to generate normal, random distributions of spawner (S) and recruit (R) bivariate pairs, with the R regime state (i.e., its distribution) depending on the threshold spawner value (S_{TH}). Each negative, randomly generated variable was discarded and replaced with the next positive value. In all simulations, if $S = 0$, then $R = 0$. The distribution of S values in each simulation had a mean of 100 and a standard deviation (SD) of 100. Thus, small and large values of S were less common than those near 100. We treated S_{TH} as a normally distributed random variable in all simulations, with its mean value depending on the modeling scenario (see below). For each scenario, S_{TH} variation was SD = 0, 10, 50, 75, and 100. Thus, for simulations in which S_{TH} varied, a unique value of S_{TH} was generated for each S,R pair. Each simulation within a

scenario generated 100 *S*,*R* pairs, with 10 simulations per threshold (S_{TH}) variation category. Thus, each simulated data set corresponded to 100 years of cohort production within a population, with each modeling scenario having 10 replicate populations.

We assumed that the variance and mean of recruits was greater for $S > S_{TH}$. Thus, the mean and variance in R depended on location relative to S_{TH}. Below S_{TH}, values of R were generated with a mean = 0 and SD = 10. Hence, below S_{TH}, small values of R were common and large values rare, which would be expected if recruits were constrained by a strong depensatory-like effect. Above S_{TH}, the mean and variation for R were identical to that of S (i.e., both mean and SD = 100), as might be expected when recruits are unlimited and density-independent mechanisms predominate (i.e., ecological release is occurring).

The position of S_{TH} relative to the mean of the normally distributed S values might affect the outcome of simulations. This is because the highest density of *S*,*R* pairs generated within each simulation likely occurred near the mean S, affecting statistical power to detect a threshold effect. Within each simulation, we generated distributions with one of two S_{TH} mean values. In one case, mean S_{TH} = 50 was lower than the mean S of 100, and thus $S < S_{TH}$ occurred relatively infrequently. In another set of simulations, we set the mean S_{TH} = 100, which was the same as the mean of the S values, causing $S < S_{TH}$ to occur more commonly.

To compare our simulated *S*–*R* relationships with actual data, we acquired 60 summary data sets from a Web site formerly maintained by Ransom A. Myers at Dalhousie University (Halifax, Nova Scotia, Canada; www.mscs.dal.ca/~myers/welcome.html). All of these data sets contained at least 11 years of spawner and recruit abundance pairs and represented a diverse array of taxa (Appendix A, Table A1).

For all data sets, we attempted to fit functional relationships using two models. The first of these is a Ricker-type model (Ricker 1975):

$$R = Se^{a(1-\frac{S}{b})}$$

in which a and b were estimated with linear regression with a multiplicative error term of e^w where w is normally distributed with a mean of 0. We used the model transformed into its linear form

$$\ln\left(\frac{R}{S}\right) = a - \left(\frac{a}{b}\right)S$$

(PROC REG, SAS Institute Inc. 2003); this model captures potential downward inflections in R at high densities of S (Ricker 1975). Given that depensation may suppress densities of recruits at low spawner densities (i.e., creating a sigmoidal shape), we also fit these data to a logistic function

$$R = \frac{R_{max}\, R_0\, e^{aS}}{R_{max} + R_0(e^{aS} - 1)}$$

in which R_0 is an intercept, R_{max} is the theoretical maximum recruit density, and a is a constant. These models were fit to data using iterative nonlinear regression with error estimated from residuals (PROC NLIN, SAS Institute Inc. 2003). All regression models were considered significant at $p < 0.05$.

In addition to fitting these data sets to functional models, a nonparametric, two-dimensional Kolmogorov–Smirnov (2DKS) test was used to locate potential S_{TH} densities where purported recruit regimes shifted from low and invariant to high and variable (Fasano and Franceschini 1987; Garvey et al. 1998). This test identifies the point (S^*, R^*) within a bivariate (i.e., S, R) distribution in which the distribution of points among the quadrants formed with S^*, R^* at the center differs the most from the expected distribution that arises when all combinations of S and R are equally likely. This point of maximum difference (i.e., that which generated the maximum value of the test statistic, D_{BKS}) corresponds to a simulated threshold breakpoint, in which variation of the dependent variable changes from constrained to relatively unconstrained at a simulated threshold point (Fig. 1; Garvey et al. 1998). In other words, the test found the maximum change in variation in the data set rather than a functional change between the two variables. If a functional relationship is underlying the bivariate relationship, then the maximum change occurs at the median value of S. The test appears to be robust to small sample sizes (Garvey et al. 1998).

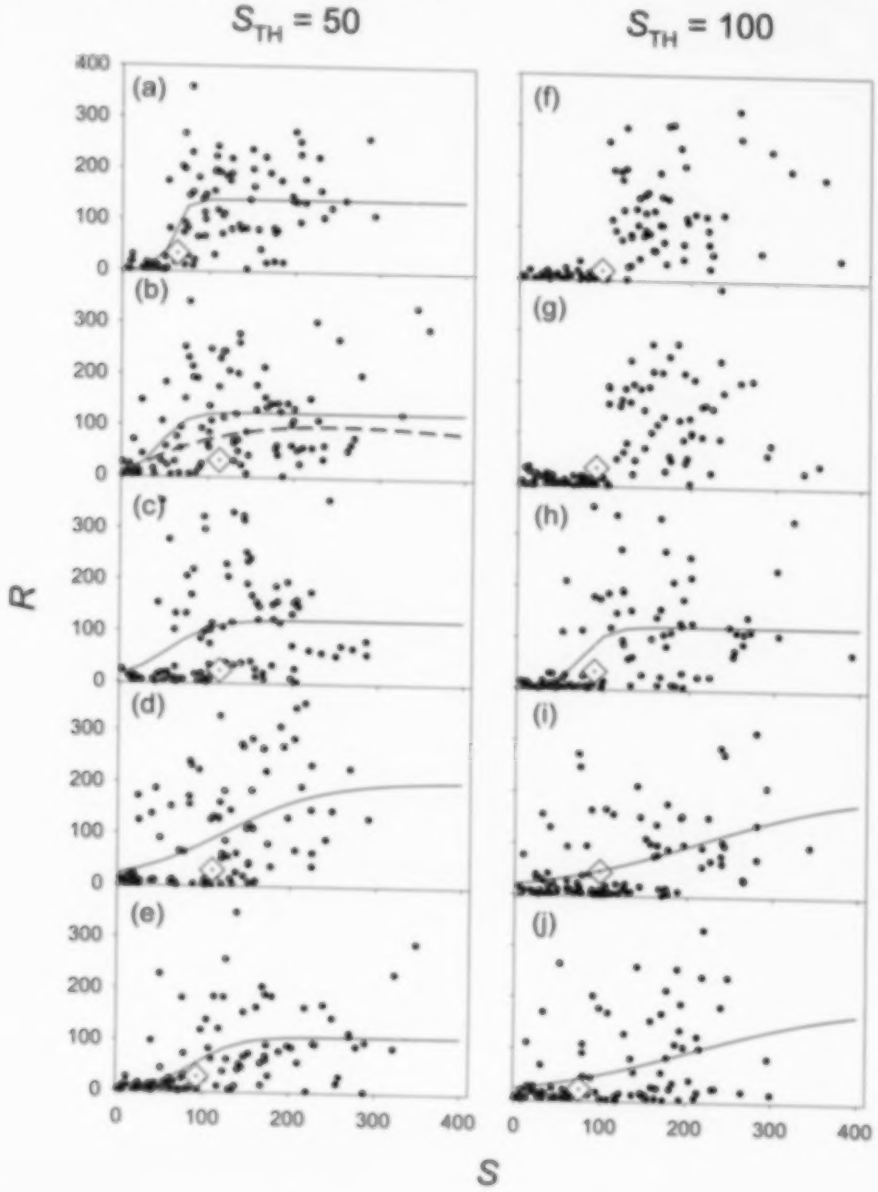
Each simulated and actual data set was analyzed using the 2DKS test, where the D_{BKS} test statistics generated for each bivariate point were calculated and compared with those for 5000 rerandomized distributions. A p value for each test was calculated as the proportion of rerandomized data sets that produced a D_{BKS} larger than the actual data set (see Garvey et al. 1998). The smallest p value was associated with the maximum D_{BKS} and associated *S*,*R* pair (S^*,R^*) for each simulated data set. We calculated the mean and standard error of S values associated with each maximum D_{BKS} value within each simulation set (N = 10), which we hypothesized reflected the true S_{TH} values that occurred between regimes of low plus invariant versus high plus variable recruit abundance.

Results

Even though the simulations had no underlying functional assumptions, patterns could sometimes be represented with Ricker and logistic models, although the fits of the models varied. When the mean S_{TH} = 50, Ricker fits were significant ($p < 0.05$) for only 6 of the 10 data sets when S_{TH} was invariant and 0 of 10 data sets when S_{TH} was highly variant with SD = 100 (see Fig. 2 for example distributions). When the mean S_{TH} = 100, Ricker fits also did not fit the simulated data well (Fig. 2). In contrast, for both mean values of S_{TH} in simulations, the logistic fits were poor when S_{TH} was invariant (Figs. 2*f*, 2*g*), but improved as S_{TH} increased in variance (Fig. 2; 75% fit across all simulations). The abrupt "knife-edge" change in recruit abundance at low variation in S_{TH} apparently prevented logistic model fits (e.g., Figs. 2*f*, 2*g*).

The S_{TH} values associated with the maximum D_{BKS} statistics in the 2DKS differed in their ability to match the true location of S_{TH} in simulations (Fig. 2). The S_{TH} mean relative to the mean of S in each simulated population affected the predicted value (Fig. 3). When the mean S_{TH} was 50, less than the expected S of 100, the 2DKS overestimated the true threshold value, with the bias increasing as the var-

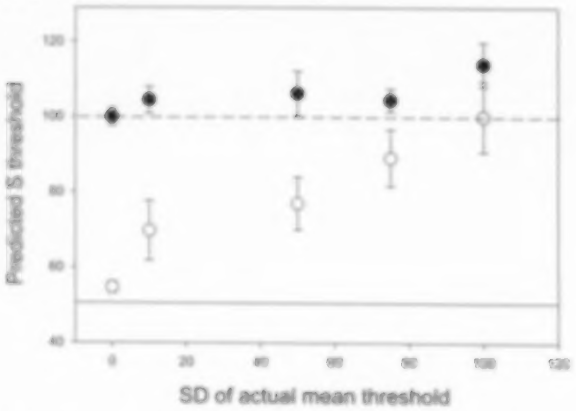
Fig. 2. Randomly chosen example distributions of spawner abundance (S) and recruit abundance (R) (N = 100 per panel; nine additional simulations were conducted for each scenario). In all of these simulations, mean and variance of R was small below the spawner threshold (S_{TH}) and high above it. In panels *a–e*, the mean S_{TH} = 50 and in panels *f–j*, mean S_{TH} = 100. The diamond on each panel depicts the predicted S_{TH} from a nonparametric 2DKS test ($p < 0.05$). The broken curve fitted through each relationship derives from a significant ($p < 0.05$) Ricker model, if one occurred. Solid curves are significant logistic model fits. (*a* and *f*) Standard deviation (SD) of S_{TH} = 0; (*b* and *g*) SD = 10; (*c* and *h*) SD = 50; (*d* and *i*) SD = 75; (*e* and *j*) SD = 100.



iance of S_{TH} increased (Figs. 2*a–2e*, Fig. 3). This bias was likely due to the relative distribution of points generated around S_{TH} and its effect on the test's ability to identify the simulated change (i.e., fewer points occurred to the left of the S_{TH}). Biased estimates did not occur when S_{TH} was 100, the same as the expected S (Figs. 2*f–2j*, Fig. 3).

Patterns within published S–R data sets were diverse (Fig. 4). The Ricker model produced significant fits through 58% of the 60 data sets, whereas the logistic model fit 11% of the populations. The 2DKS test found significant apparent breakpoints in 45% of the data sets. The Ricker and 2DKS jointly found significant relationships in 33% in the subset

Fig. 3. Mean ± standard error of predicted threshold spawner density (S_{TH}) that produced the largest test statistic in each simulation ($N = 10$ simulations per mean) as a function of variation in the true S_{TH} values. The solid horizontal line is $S_{TH} = 50$ (predicted means, open circles), and the broken line represents $S_{TH} = 100$ (solid circles).



of data sets in which one test found a relationship. The logistic and 2DKS shared significant results for 55% of the significant data sets.

Breakpoints identified by the 2DKS appeared to locate meaningful changes in variation that could be qualitatively categorized in all of the example data sets (Fig. 4). For alewife (*Alosa pseudoharengus*) and capelin (*Mallotus villosus*) examples, R was low below the purported S_{TH}; the average R increased past the breakpoint (Figs. 4*a*, 4*b*). A significant Ricker relationship also could be fit to these data (Figs. 4*a*, 4*b*). A logistic model fit the capelin data, but the fit was poor (Fig. 4*b*). In bluefin tuna (*Thunnus thynnus*), Atlantic cod (*Gadus morhua*), and Atlantic herring (*Clupea harengus*) S–R distributions, the mean and variance in R was constrained below the purported S_{TH} (Figs. 4*c*–4*e*). Above the S breakpoint, S and R were positively related for these species (Figs. 4*c*–4*e*). For herring, both Ricker and logistic models could be fit to the data (Fig. 4*e*). Both mean and variation of recruits were constrained below the S_{TH} for red king crab (*Paralithodes camtschaticus*) and lake whitefish (*Coregonus clupeaformis*) (Figs. 4*f*, 4*g*). A Ricker fit occurred for the red king crab data set and a logistic fit for the lake whitefish data (Figs. 4*f*, 4*g*). For pink salmon (*Oncorhynchus gorbuscha*), only a breakpoint could be identified (Fig. 4*h*). In most of these example data sets, the apparent clustering of recruits at low densities below the S breakpoint (notably Figs. 4*c*, 4*d*, 4*e*, 4*f*, 4*g*) was a pattern similar to that generated by our discontinuous simulations (Fig. 2).

Discussion

Conventional wisdom holds that smooth, continuous functions underlie relationships between adults and offspring production in populations and that these functions ultimately shape population dynamics. Conversely, our results show that it is plausible that rapid, discontinuous shifts in reproductive output at some threshold region of adult density affect recruitment success. As our simulations and some of the actual data sets demonstrated, in the absence of underlying mechanistic data (e.g., experimentally derived), it may be difficult to ascertain under what circumstances the assumption of continuous versus discontinuous processes is appropriate.

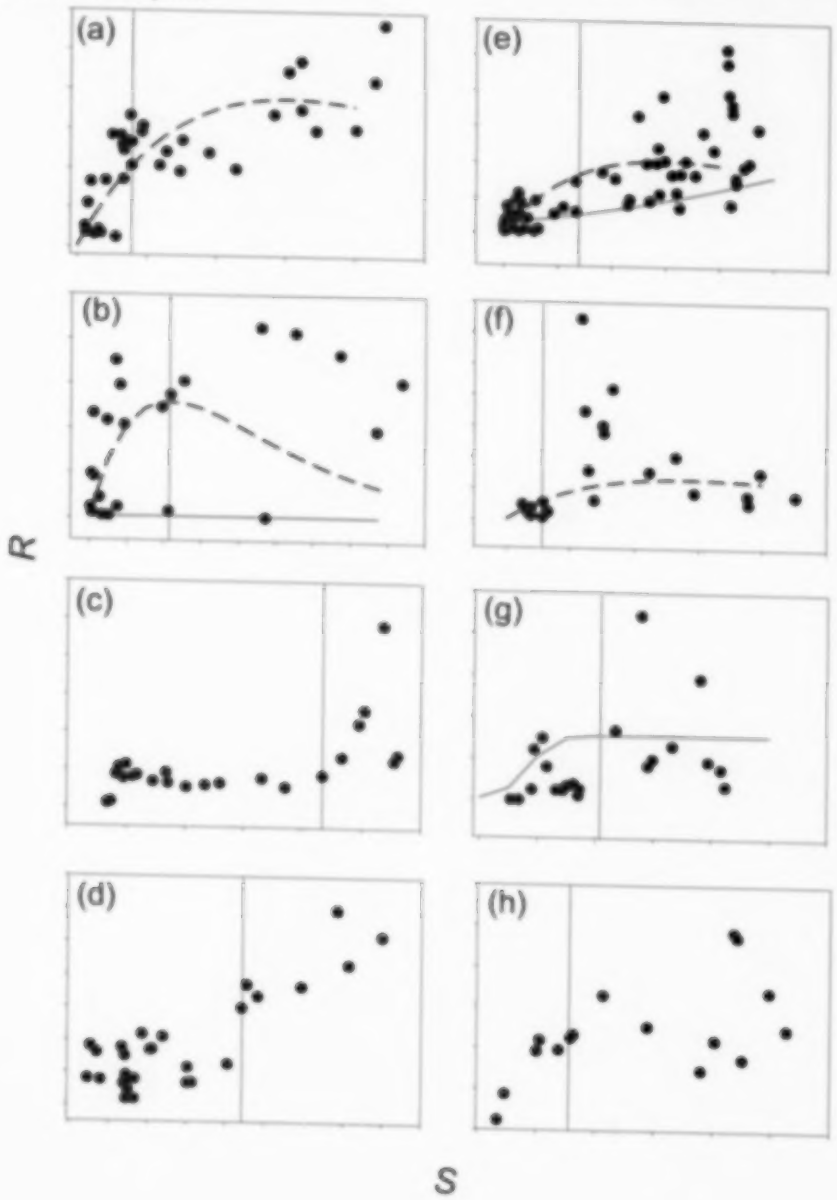
Assumptions about underlying ecological relationships have important implications for managing risk (Walker and Meyers 2004). Fisheries management strategies often depend on setting allowable harvest to permit sufficient escapement of spawners. These surviving adults then live on to generate sustainable and strong year classes of recruits. Traditionally the spawner to recruit relationship has been characterized with various continuous functional models that seek to find the appropriate target adult density that ensures high recruitment in the future, with limited success (Hilborn et al. 1995). A possible reason for failure is that these models assume that recruitment within populations exists along a continuum of equilibrium states across a range of adult densities, creating predictable management scenarios. However, if populations have discrete stable recruitment regime states depending on regions of spawner density, then assuming that continuous functional relationships apply through the entire data set may generate erroneous management decisions.

Rather than assuming smooth underlying relationships, using tools that identify how adult abundance affects the mean and variation in recruit abundance may be more appropriate. In fact, as our simulations and some of the published data sets suggest, statistical models such as the Ricker, with compensatory assumptions, and the logistic, which incorporates a depensatory-like response at low densities, may find continuous S–R relationships when patterns are in reality driven by abrupt, discontinuous changes in recruitment state. Thus, approaches for finding breakpoints in bivariate data such as the 2DKS and others (e.g., biphasic linear regression, Nickerson et al. 1989; maximum likelihood modeling, Beckage et al. 2007) may be necessary for defining important regime state shifts or identifying abrupt functional changes within fish populations and other ecological systems. Many ecological mechanisms occurring at the population, community, and perhaps ecosystem level may have affected individual reproductive output and caused the abrupt changes.

Although real biological reasons may exist for threshold changes in spawner–recruit relationships, the ability for the statistical test we used (as well as others) to identify the true threshold depends on complex factors, including underlying sampling distributions. Our simulations showed that the 2DKS test would yield conservatively inaccurate estimates of the true threshold spawning density under specific circumstances. Although this may lead to risk-averse management, it also may result in economically costly limitations to fishery yield. Thus, in addition to using statistical tools to identify putative shifts in spawner–recruit relationships, our results underscore the need to understand causal mechanisms.

For other data sets, underlying relationships between spawners and recruits may have been continuous, rendering the assumption of a threshold change false, even if the 2DKS identified a breakpoint. In these continuous relationships, the 2DKS was simply identifying some point of central tendency in the bivariate distribution (i.e., the median);

Fig. 4. Spawner (*S*) and recruit (*R*) relationships for eight example fisheries out of 60 (Appendix A, Table A1). Panels correspond to data in Appendix A: (*a*) alewife (*Alosa pseudoharengus*, data set 1), (*b*) capelin (*Mallotus villosus*, data set 8), (*c*) bluefin tuna (*Thunnus thynnus*, data set 6), (*d*) Atlantic cod (*Gadus morhua*, data set 13), (*e*) Atlantic herring (*Clupea harengus*, data set 27), (*f*) red king crab (*Paralithodes camtschaticus*, data set 48), (*g*) lake whitefish (*Coregonus clupeaformis*, data set 35), and (*h*) pink salmon (*Oncorhynchus gorbuscha*, data set 43). The vertical line in each panel depicts the *S* that produced the maximum difference in each 2DKS test. The broken (Ricker) and solid (logistic) curves fitted through each relationship derive from a significant ($p < 0.05$) regression model, if one occurred. Axes values differ among data sets and are not depicted.



the spawner–recruit patterns likely were nonlinear because of density-dependent feedbacks within the population (Myers 2002), with no abrupt shift in recruits. A candidate from our example data sets may have been the alewife pattern, as identified by its strong Ricker model fit. At low densities of adults, reduced intraspecific competition may have improved adult condition and enhanced birth rates (i.e., classic compensation). As adult abundance ascended toward some purported carrying capacity, birth rates declined (Myers 2002), causing recruit production to decelerate. Off-

spring survival also may have declined as intracohort competition (Rettig and Mittelbach 2002) or predation (Forney 1976) increased.

It is also possible that continuous relationships may apply across only a subset of spawner densities and that tests such as the 2DKS find this transition. For example, the apparent decline in mean *R* past some intermediate density of *S* in some of the populations (particularly for red king crab) may be explained by density-dependent responses at high *S*, which we did not incorporate in our simulations. Similarly, the linear increase in recruits above the purported spawner breakpoint for Atlantic herring suggests a lack of compensatory feedback and perhaps a lognormal increase in variation of recruits produced, which again were not incorporated in our simulations.

When they occur, putative threshold spawner densities that affect recruitment state within a fishery may change among years and populations. Our simulations demonstrated that this variation might cause discontinuous relationships between spawners and recruits to appear to be smooth if the spawner threshold varies markedly. For example, behavior of fishers and their impact on spawners may vary among years depending on factors affecting fishing profitably and success (Bettoli et al. 2007). Other factors such as climate, food quality, and reproductive habitat that vary among years and populations may influence the point at which recruitment is constrained by adult abundance. Identifying variability around the average spawner threshold would allow us to bracket the region of spawner densities that fundamentally different recruitment mechanisms (e.g., biotic versus abiotic) are at play. Appropriate modeling and research may then be directed toward identifying underlying processes (Muradian 2001; Bestelmeyer 2006).

An unfortunate characteristic of all our example relationships is that spawner abundance declined to such a point that the mean and variation in recruits were constrained, and presumably these populations reached a state of low spawner and recruit density. Thus, to identify such relationships, either environmental conditions or harvest must have been sufficiency deleterious to deplete adult densities and perhaps cause populations to fall into an apparent, low-recruitment regime state. Obviously, allowing recruits to decline to identify the critical spawner threshold is not a desirable management scenario. Further, recovery of these populations to high recruitment states may be difficult. Once populations have reached a low recruitment state, lags may exist in the response of recruitment to increasing spawner densities and favorable external factors. Within populations, genotypes that favor reproductive phenotypes with high inherent reproductive output (late maturation, high fecundity) may be rare and take time to increase in populations as adult densities rise (Jennings et al. 1997; Walsh et al. 2006). At the community level, an increase in sympatric predators and competitors at low recruit abundance may suppress the ability for recruit production to rapidly increase if spawner densities increase past the purported spawner threshold (Walters and Kitchell 2001). At the ecosystem scale, adult-driven feedbacks to food webs may be absent, preventing recruitment from successfully occurring.

It is our hope that the 2DKS test and others that detect breakpoints in bivariate data might be used to identify apparently discontinuous relationships and potential recruitment regimes in existing distributions. It would drive mechanistic research into the nature of apparent adult reproductive thresholds and allow managers to avoid these conditions in other populations in which such possible regime shifts have not yet occurred (Post et al. 2002). In other words, the goal would be to keep populations from reaching regions of spawner densities that cause regimes of low recruitment potential. As a heuristic tool, the ability for the 2DKS test and others to identify inflections may allow researchers to design models or experiments to understand under what conditions internal dynamics within populations versus external environmental factors drive the production of cohorts.

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Appendix A

Table A1. List of spawner (*S*) and recruit (*R*) data used in analyses of patterns with a Ricker model and a nonparametric, two-dimensional Kolmogorov–Smirnov (2DKS) test.

No.	Species	Location	*S*	*R*
1	*Alosa pseudoharengus*	Atlantic Ocean, Damariscotta River	Biomass	Numbers
2	*Alosa pseudoharengus*	Atlantic Ocean, Saint John River	Biomass	Numbers
3	*Alosa pseudoharengus*	Atlantic Ocean, Saint John River	Numbers	Numbers
4	*Engraulis mordax*	Pacific Ocean, California	Biomass	Numbers
5	*Alosa sapidissima*	Atlantic Ocean, Connecticut River	Numbers	Numbers
6	*Thunnus thynnus*	West Atlantic	Biomass	Numbers
7	*Mallotus villosus*	Iceland	Biomass	Index
8	*Mallotus villosus*	Barents Sea	Biomass	Numbers
9	*Mallotus villosus*	Barents Sea	Biomass	Index
10	*Mallotus villosus*	Barents Sea	Biomass	Index
11	*Oncorhynchus tshawytscha*	Alaska, Blossom River	Numbers	Numbers
12	*Oncorhynchus tshawytscha*	Alaska, Chickamin River	Numbers	Numbers
13	*Gadus morhua*	North Atlantic, NAFO 2J3KL	Biomass	Numbers
14	*Gadus morhua*	North Atlantic, NAFO 3NO	Biomass	Numbers
15	*Gadus morhua*	North Atlantic, NAFO 3PN4RS2	Biomass	Numbers
16	*Gadus morhua*	North Atlantic, NAFO 3Ps4RS	Biomass	Numbers
17	*Gadus morhua*	North Atlantic, NAFO 3PS	Biomass	Numbers

Table A1 (*concluded*).

No.	Species	Location	*S*	*R*
18	*Gadus morhua*	North Atlantic, NAFO 4tvn	Biomass	Numbers
19	*Gadus morhua*	North Atlantic, NAFO 4vsw	Biomass	Numbers
20	*Gadus morhua*	North Atlantic, NAFO 5Y2	Index	Index
21	*Gadus morhua*	North Atlantic, NAFO 5Z	Biomass	Numbers
22	*Gadus morhua*	Baltic Ocean	Biomass	Numbers
23	*Gadus morhua*	Baltic Ocean	Biomass	Numbers
24	*Gadus morhua*	Iceland	Biomass	Numbers
25	*Gadus morhua*	North Sea	Biomass	Numbers
26	*Gadus morhua*	North Atlantic	Biomass	Numbers
27	*Clupea harengus*	Downs Stock	Biomass	Numbers
28	*Clupea harengus*	Georges Bank	Biomass	Numbers
29	*Clupea harengus*	Gulf of Maine	Biomass	Numbers
30	*Clupea harengus*	Vancouver Island	Biomass	Numbers
31	*Clupea harengus*	Alaska	Biomass	Numbers
32	*Clupea harengus*	Alaska	Adult eggs	Numbers
33	*Clupea harengus*	Vancouver Island (SW)	Biomass	Numbers
34	*Scomberomorus cavalla*	Gulf of Mexico	Numbers	Numbers
35	*Coregonus clupeaformis*	Lake Huron	Adult eggs	Index
36	*Coregonus clupeaformis*	Lake Superior	Biomass	Numbers
37	*Coregonus clupeaformis*	Whitefish Bay, Lake Superior	Biomass	Numbers
38	*Scomber scombrus*	North Atlantic	Biomass	Numbers
39	*Scomber scombrus*	Black Sea	Biomass	Numbers
40	*Brevoortia tyrannus*	US Atlantic	Female biomass	Numbers
41	*Brevoortia patronus*	Gulf of Mexico	Biomass	Numbers
42	*Engraulis ringens*	Peru	Biomass	Numbers
43	*Oncorhynchus gorbuscha*	Auke Creek, Alaska	Numbers	Numbers
44	*Oncorhynchus gorbuscha*	Bakhura River	Numbers	Numbers
45	*Oncorhynchus gorbuscha*	Aristazabal Is., British Columbia	Numbers	Numbers
46	*Oncorhynchus gorbuscha*	Bentinck, British Columbia	Numbers	Numbers
47	*Oncorhynchus gorbuscha*	Alaska	Numbers	Numbers
48	*Paralithodes camtschaticus*	Bristol Bay, Alaska	Biomass	Numbers
49	*Sardinops sagax*	California	Biomass	Numbers
50	*Sardinops sagax*	Gulf of California	Numbers	Numbers
51	*Sander vitreum*	Balsam Lake, Ontario	Index	Index
52	*Sander vitreum*	Lake Erie	Index	Index
53	*Sander vitreum*	Lake Erie	Numbers	Numbers
54	*Sander vitreum*	Lake Erie	Index	Index
55	*Coregonus lavaretus*	Lake Constance, Europe	Numbers	Numbers
56	*Theragra chalcogramma*	Gulf of Alaska	Biomass	Numbers
57	*Theragra chalcogramma*	West Bering Sea	Biomass	Numbers
58	*Pleuronectes ferrugineus*	North Atlantic	Biomass	Numbers
59	*Thunnus albacares*	Eastern Pacific Ocean	Biomass	Numbers
60	*Thunnus albacares*	Indian Ocean	Numbers	Numbers

Note: Each data set contains at least 11 years worth of cohort data.

A sequential Bayesian methodology to estimate movement and exploitation rates using electronic and conventional tag data: application to Atlantic bluefin tuna (*Thunnus thynnus*)

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Abstract: This paper presents a Bayesian methodology to estimate fishing mortality rates and transoceanic migration rates of highly migratory pelagic fishes that integrates multiple sources of tagging data and auxiliary information from prior knowledge. Exploitation rates and movement rates for Atlantic bluefin tuna (*Thunnus thynnus*) are estimated by fitting a spatially structured model to three types of data obtained from pop-up satellite, archival, and conventional tags for the period 1990–2006 in the western North Atlantic. A sequential Bayesian statistical approach is applied in which the key components of the model are separated and fitted sequentially to data sets pertinent to each component with the posterior probability density function (pdf) of parameters from one analysis serving as the prior pdf for the next. The approach sequentially updates the estimates of age-specific fishing mortality rates (F) and transoceanic movement rates (T). Estimates of recent F are higher than the estimated rate of natural mortality and higher in the east than in the west. Estimates of annual T from the west to the east are higher for larger fish (6% for ages 0–3 to 16% for ages 9+). These estimates are also higher than those obtained from tagging studies before the 1990s and could be associated with changes in stock composition.

Résumé : Notre travail présente une méthode bayésienne pour estimer les taux de mortalité dus à la pêche et les taux de migration transocéanique de poissons pélagiques fortement migrateurs qui intègre de multiples sources de données de marquage et des informations auxiliaires provenant de connaissances antérieures. Nous estimons les taux d'exploitation et de déplacement des thons rouges (*Thunnus thynnus*) en ajustant un modèle à structure spatiale à trois types de données provenant d'étiquettes satellites détachables, d'étiquettes enregistreuses et d'étiquettes ordinaires durant la période 1990–2006 dans l'ouest de l'Atlantique Nord. Nous utilisons une approche statistique bayésienne séquentielle dans laquelle les composantes essentielles du modèle sont séparées et ajustées séquentiellement à des ensembles de données pertinentes à chaque composante et dans laquelle la fonction de densité de probabilité (pdf) a posteriori des paramètres d'une analyse servent de pdf a priori pour l'analyse suivante. Cette approche remet à jour séquentiellement les estimations des taux de mortalité dus à la pêche en fonction de l'âge (F) et les taux de déplacements trans-océaniques (T). Les estimations des F récents sont supérieures aux taux estimés de mortalité naturelle et plus élevées dans l'est que dans l'ouest. Les estimations du T annuel de l'ouest vers l'est sont supérieures pour les poissons plus grands (6 % aux âges 0–3 à 16 % aux âges 9+). Ces estimations sont aussi supérieures à celles faites à partir des études de marquage antérieures aux années 1990 et pourraient être reliées à des changements de composition de stocks.

[Traduit par la Rédaction]

Introduction

Mark–recapture data sets enable estimation of movement and exploitation rates if tagged fish are representative of the target population, if all recaptured tags are reported or the reporting rate is known, and if the behavior of the fish is not impacted by tagging (Pollock 1991; Sibert et al. 1999; Pine et al. 2003). Uniquely identified conventional tags have long been used in fisheries to investigate mortality rates, population size, growth rates, and movement (Quinn and Deriso 1999; Walters and Martell 2004). More recently, electronic tags, which provide detailed and continuous infor-

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mation such as light level, location, pressure, and temperature data, have been developed and applied mainly to highly migratory species such as tunas (Block et al. 1998, 2001, 2005). Pop-up satellite archival tags (or "pop-up satellite tags") are a unique fisheries-independent tag developed specifically to examine movements without the bias of fisheries interactions. Subject to a limit on information transfer due to bandwidth and battery capacity, the tags summarize archived data and transmit information to a satellite. To date, most tracks on bluefin tuna range from 1 to 9 months. In contrast, implanted archival tags (or "archival tags") offer the advantage of long-term retention and retrieval of a higher-resolution time series for up to several years. Both of these electronic tags have been used extensively to investigate fish movement patterns, behavioral ecology, and thermal biology (Weng et al. 2005; Wilson et al. 2005; Schaefer et al. 2007). Compared with conventional tagging experiments, the number of electronic tags released in a program is often limited because deployment and recapture of these tags are expensive. Electronic tag data, however, can be used to estimate mortality rates because they have an advantage over conventional tags in that reporting rates are expected to be higher due to higher tag-return rewards and enhanced publicity. To date, however, there has been very little research seeking to estimate exploitation rates from electronic tag data.

Bluefin tuna are one of the most economically valuable fish in the world, with prices reaching US$1000/kg in the Tokyo Tsukiji market. Because of its declining stock status, research on and fisheries management of Atlantic bluefin tuna (*Thunnus thynnus*) in the North Atlantic Ocean have received a great deal of attention (ICCAT (International Commission for the Conservation of Atlantic Tunas) 2007; Kell and Fromentin 2007), including an extensive electronic tagging campaign (Block et al. 2005; Wilson et al. 2005). ICCAT regulates the fishery by setting annual quotas for each member country in each of two management zones (separated by the 45 W meridian): (*i*) the Western Atlantic and (*ii*) the Eastern Atlantic and Mediterranean Sea. In the western Atlantic, the main fishing fleets are rod-and-reel, longline, and purse seine, and in the east, there are a variety of fleets such as purse seine, bait boat, trap, and longline. There have, however, been controversies regarding the population structure and the current level of transoceanic migrations. Conventional tag programs conducted for small fish (mainly ages 1–3) by USA since 1954 (Mather et al. 1995) have indicated low trans-Atlantic migration rates from west to east (about 1%; National Research Council (NRC) 1994). In contrast, archival and pop-up satellite tag research, which targeted larger fish released in the western Atlantic (mainly ages 7–10), showed higher occurrence of transoceanic migrations (Block et al. 2001, 2005). Additionally, these researchers identified that there are at least two population components involved in trans-Atlantic movements, which have different spawning grounds (the Gulf of Mexico and the Mediterranean Sea), further complicating estimations owing to mixing on foraging grounds.

In recent ICCAT stock assessments, an ADAPT virtual population analysis (VPA) model (ICCAT 2007) has been used to provide management advice. Although this is applied to fisheries catch-at-age data and various abundance indices, it does not incorporate tagging information and currently ignores any mixing of stocks. Migration rates are key factors in estimating exploitation rates in metapopulation situations (Walters and Martell 2004). They can also influence the defining of the boundaries in management zones. Therefore, for better stock management, it is essential to develop new models of fishing mortality and the transoceanic migration rates using all sources of tagging data.

Bayesian state–space models are among the most powerful tools for fishery stock assessments when available data and information are sparse (Meyer and Millar 1999; Rivot et al. 2004). They offer a statistically rigorous approach to account for and reduce uncertainties by providing a probabilistic framework and incorporating both process and observation (measurement) errors. Recently, quantitative stock assessment models with many parameters have been developed to integrate multiple data sources (e.g., Hampton and Fournier 2001; Maunder and Watters 2003). It is common for a single model to be fitted to all available data sets at one time for parameter estimation. This, however, may complicate reaching and identifying numerical convergence and introduce computational burden, owing to the estimation of many parameters, although there are some techniques to diminish these problems (e.g., some of the parameters can be fixed initially to get reasonable starting values for the other parameters). To overcome the challenges of combining multiple data sources and auxiliary information, a sequential Bayesian approach (Gelman et al. 2004) has been proposed and applied in stock assessments (Myers and Mertz 1998; Michielsens et al. 2008). In the sequential approach, different data sets can be analyzed separately with models specialized for each data set. By using posterior distributions of parameters of interest as prior probability density functions (pdfs) in subsequent analyses, multiple data sets and auxiliary information can be integrated efficiently and reliably.

In this paper, a state–space tagging model (e.g., Mäntyniemi and Romakkaniemi 2002; Michielsens et al. 2006) that follows a sequential Bayesian estimation approach is presented and illustrated with an application to Atlantic bluefin tuna. Exploitation rates and transoceanic movement rates from 1990 to 2006 are estimated from two types of electronic tags, pop-up satellite tags and archival tags, as well as from conventional tag data sets. These three types of tags have different characteristics in terms of information provided on movements and mortality by age. In addition, they each provide information on the fisheries dependence in tag recapture. The statistical analyses of these data provide estimates of area- and age-based fishing mortality rates that account for movement rates by age.

Materials and methods

A spatially and age-structured model is formulated that tracks the fate of each tagged group defined by tag type, release year, release area, and age. A Bayesian state–space estimation approach is applied that treats all estimated parameters as random variables and requires a prior pdf (or "prior") to be assigned to the estimated variables. It estimates fishing mortality rate, F, in each area by age group, tag reporting rates by tag type, and annual crossover rates by age group. The rate of natural mortality, M, is also

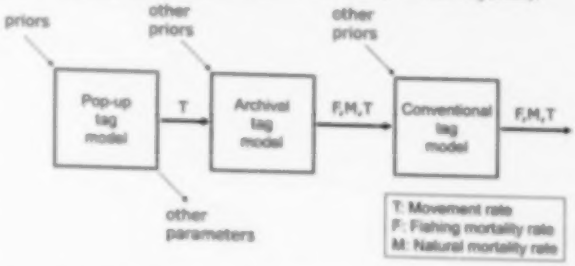
treated as a random variable but with high prior precision. In the state–space modeling framework, both observation error and process error are explicitly modeled.

The empirical basis for parameter estimation derives from the comparison of model predictions with observations of the number of tags of a given tag type recaptured in a given area. Pop-up satellite, archival, and conventional tags are modeled separately, and different assumptions are made about the information contained in each tag type and about tag fate. For example, the key process modeled for pop-up satellite tags is movement. In contrast, for internally implanted archival tags and externally placed conventional tags, the recapture observation is treated as a reported fishing mortality event. Further structural assumptions are made about tag reporting rates. It is assumed that tag reporting rates are higher for archival tags than for conventional tags primarily due to the enhanced reward structure that provides US$1000 for archival tags versus a hat for conventional tags.

A sequential Bayesian approach (Michielsens et al. 2008) is formulated to integrate information from the three kinds of tags. This approach consists of three parts in the current study (Fig. 1). First, the posterior pdfs of movement rates are estimated from pop-up satellite tag data along with other nuisance parameters. Next, the posterior pdf of movement rates is used as the prior pdf of these parameters for archival tag modeling, which in turn will provide posteriors of movement rates and fishing mortality rates. These estimates are for after 1997, when the archival tag data started to accumulate. Finally, the posterior from the archival tag modeling is used as the prior for conventional tag modeling. The distributions of estimates including fishing mortality rates between 1990 and 1996 are updated by conventional tag information. The sequential order of the analysis of the three kinds of tags was determined according to model input requirements and to most readily facilitate numerical convergence of the Markov chains. The pop-up satellite tag model was simplest and had the fewest input requirements and was thus analyzed first. The archival tag model was intermediate in complexity and could utilize the key posterior outputs of the pop-up satellite tag model as priors. The conventional tag reporting rates were conditional on values for reporting rates of archival tags, and it was thus necessary to run the archival tag model before the conventional tag model. If suitable priors could be formulated, however, parameters could be estimated simultaneously in a single model without applying the sequential approach. The archival and conventional tag data sets may be good candidates for this alternative approach because the model structure applied to them is almost same.

We have selected 1990 as the starting year because the model applied assumes consistency of fishing patterns and tagging activities in its estimation of parameters, and fishing operation patterns are considered to have changed with rapidly increasing catches after 1990. Conventional tagging on Atlantic bluefin tuna in the Western Atlantic started in the 1950s and was conducted actively in the 1960s–1970s and 1990s. However, there were few tag releases in the 1980s, which provides another reason for setting the starting year as 1990. Many of the tags in the 1990s were released in a common set of experiments in which fish were tagged with conventional, archival, or satellite tags in the winter fishery off North Carolina.

Fig. 1. Framework of the Bayesian sequential approach that was applied in the analysis of pop-up satellite, archival, and conventional tagging data for Atlantic bluefin tuna (*Thunnus thynnus*).



Data

Release and end point data of the three kinds of tags are used for modeling. The full track data available from the application of geolocation algorithms used to estimate a track from archival and pop-up satellite tags are not used in this current analysis, despite being of high value for understanding fine-scale detail in migration patterns. We envision a two-step approach for the incorporation of tag data sets that contain migration patterns. We regard this paper as the first step in a longer-termed, multistage research effort to develop mathematical approaches for modeling these novel types of tagging data. The release and endpoint location for pop-up reporting to satellite or fisheries recapture are categorized into two spatial areas (west and east) in the North Atlantic Ocean separated by the 45th degree W meridian. We use the same definition as the ICCAT geographical delimitation, because it is necessary to examine the validity of this zone definition and evaluate the low migration rate hypothesis.

Pop-up satellite tag

Pop-up satellite tags were attached to Atlantic bluefin tuna (ages 4–16, mainly 7–10) using monofilament leaders and titanium darts (Block et al. 2001, 2005). These tags record information on light levels, ambient water temperature, and pressure and, to date, are attached to bluefin tuna for less than a year. The tags detach on a user-defined date, or when prematurely released, and transmit archived data to Argos satellites. The Argos satellite system calculates the pop-up endpoint locations of the tags using the Doppler shift of the radio transmissions (Taillade 1992). In the current generations of pop-up satellite tags, the tag will detach from the fish if the animal goes below a preset depth or remains at a constant depth (e.g., as if on the bottom or at the surface for a user-set number of hours), which often is indicative of fish mortality or premature detachment of the tag. We examined 320 records from pop-up satellite tags deployed on Atlantic bluefin tuna that successfully popped up from 1997 to 2006 in 22 independent tagging campaigns by the TAG-A-GIANT program of the Tuna Research and Conservation Center (TRCC) (Table 1). In this set of deployments, 296 pop-up satellite tags were deployed in the western Atlantic management unit and 24 were deployed in the eastern Atlantic. The results were compiled to represent

Table 1. The number of tag releases and return rates (%; number of reported recaptures / number of releases) by age groups (ages 0–3, 4–8, and 9+) for three tags used for this analysis.

	Pop-up tag				Archival tag				Conventional tag					
	No. releases		Return rate		No. releases		Return rate		No. releases			Return rate		
	4–8	9+	4–8	9+	4–8	9+	4–8	9+	0–3	4–8	9+	0–3	4–8	9+
1990									212	97	2	6.6	6.2	0.0
1991									733	59	7	4.1	1.7	0.0
1992									754	59	2	4.1	8.5	0.0
1993									434	101	7	5.8	5.9	0.0
1994									88	141	69	6.8	9.9	10.1
1995									640	315	309	8.4	6.0	7.1
1996									246	933	197	1.6	6.5	2.5
1997	35	1	91.4	100.0	153	5	26.8	0.0	650	1148	125	4.9	6.3	7.2
1998	0	8		75.0					1433	89	48	3.9	0.0	6.3
1999	1	3	100.0	0.0	73	36	30.1	33.3	327	210	19	2.1	0.5	5.3
2000	32	21	71.9	52.4					148	307	5	2.7	1.3	0.0
2001	47	37	68.1	78.4					151	132	15	0.7	1.5	0.0
2002	49	14	89.8	92.9	17	1	17.6	0.0	340	135	16	2.1	1.5	12.5
2003	12	9	100.0	88.9	99	8	16.2	12.5	239	17	24	0.8	5.9	0.0
2004	0	19		89.5	50	43	4.0	9.3	1404	14	32	0.4	0.0	0.0
2005	2	26	100.0	84.6	45	20	2.2	0.0	152	9	27	0.0	0.0	0.0
2006	1	3	100.0	66.7	2	3	0.0	0.0	79	10	5	2.5	0.0	0.0

the numbers of tags that had popped off in each of the two spatial areas.

Archival tag

Archival tags were surgically implanted into the peritoneal cavity of the fish (Block et al. 2001, 2005). The archival tags deployed measured light intensity, depth, ambient seawater temperature, and peritoneal temperatures for up to 5 years. The tags require recapture to recover the time series data set. The endpoint locations of the tags were reported by the fishers recapturing the fish. In this analysis, 556 archival tags deployments from 11 tagging experiments conducted by the TAG-A-GIANT program were compiled (Table 1). All tags available for the analysis were released in the western Atlantic management area. All 101 recapture records (data up until 2006) have information on recapture locations and dates. The age range of the fish with archival tags is from 4 to 13 years of age (primarily from 7 to 10).

Conventional tag

We examined conventional tag data recently made available by the US National Marine Fisheries Service (NMFS). Data from other Atlantic bluefin tuna tagging activities (releases from the eastern Atlantic Ocean) were not used. The ICCAT tagging database includes a number of conventional tags released mainly from Spain in the early 1990s. The tag return rate (total number recaptured and reported / number released), however, was very low and most of the recaptures occurred within one year in Spain. Therefore we suspected that this tagging program might not reflect the eastern area as a whole and we refrained from incorporating the data released in the east into the current model. The NMFS database included 45 223 release records since 1954. In this analysis, 12 715 tags that were released after 1990 and had exact records of date, location, and fish length at release were analyzed (Table 1). We checked the database to remove duplicates or ambiguities. Return rates in the late 1960s were about 30% but declined to <10% in the 1990s. In particular, return rates after 1999 were very low (less than 5%). This could be interpreted as a decrease in fishing mortality and (or) reporting rate (for other possibilities, see Discussion). The majority of conventional tags were attached to juvenile fish of ages 1–2. In recent years, in conjunction with the TAG-A-GIANT program, as well as the winter Carolina fishery resurgence in the mid-1990s, several thousand conventional tags were deployed on larger fish of ages 4+.

For all three tag types, the age of tagged and recaptured fish was estimated based on measured length at deployment. The age–length growth models of Turner and Restrepo (1994) and Cort (1991) were used to estimate the age of fish released in the west and east, respectively. In this analysis, the uncertainty of the age determination was not considered. As explained later, the present model estimates fishing mortality and movement rates for three age categories, instead of each age. Thus, the effect of any uncertainty in age estimation on the final estimates was considered to be small.

Population dynamics

Basic structure

This age-structured model included two spatial areas and had an annual time step for archival and conventional tags and quarterly time steps for pop-up satellite tags. All satellite tag records had a reporting pop-up date within a year of release. All fleets in each area were aggregated, ignoring any differences in reporting rates and harvest rates between fleet types. It was presumed that movement occurred earlier in each time step, and afterwards, natural mortality and fishing mortality were experienced by the fish. This model does not account for genetic stock structures, and all fish are

Table 2. Lists of indices, model variables, data, and model parameters used for this analysis.

Symbol	Description
Indices	
c	Tag type (1, pop-up satellite tag; 2, archival tag; 3, conventional tag)
Y	Release year
a	Fish age or age group (1, ages 0–3; 2, ages 4–8; 3, ages 9+)
A	Release area (1, west of the 45°W meridian; 2, east of 45°W meridian)
i, j	Area
t	Time step (year) or time period (years)
b	Quarter programmed for pop-up tags to release
d	Quarter at liberty of tagged fish within a year (1, 0–3 months; 2, 4–6 months; 3, 7–9 months; 4, 10–12 months)
Model variables	
$N_{c,Y,a,A,i,t}$	Expected number of fish carrying tag type c, released in year Y, of age a, released in area A, residing in area i at the beginning of year t
$N^{*}_{c,Y,a,A,i,t}$	Expected number of fish carrying tag type c, released in year Y, of age a, released in area A, residing in area i after fish movement in year t
$C^{\phi}_{1,Y,a,A,i,b,d}$	Expected number of pop-up tags that successfully transmit stored data that were released in year Y, in area A, reside in area i, after d quarters that were programmed to release in the bth quarter at liberty
$C^{\phi}_{c,Y,a,A,i,t}$	Expected number of tags of type c (c = 2, 3), recovered from fish released in year Y, in area A, of age a, recaptured in area i, at year t
Data	
$L^{o}_{c,Y,a,A,b}$	Observed number of tags released, tag type c, year Y, age a, release area A. An additional subscript is added for pop-up tags programmed to pop off in the bth quarter after release.
$C^{o}_{1,Y,a,A,i,b,d}$	Observed number of pop-up tags that successfully transmit stored data that were released in year Y, in area A, reside in area i, after d quarters that were programmed to release in the bth quarter at liberty
$C^{o}_{c,Y,a,A,i,t}$	Reported number of tags of type c (c = 2, 3), recovered from fish released in year Y in area A, of age a, recaptured in area i, at year t
Model parameters	
$P_{a,i}$	Probability that a fish of age a stays in area i for a quarter
$T^{*}_{a,i,j,d}$	Movement rate of fish of age a from area i to area j or staying in the same area (in the case of $j = i$) within the first d quarters of the year
$T_{a,i,j}$	Movement rate of fish of age a from area i to area j or staying in the same area (in the case of $j = i$) in a year
$F_{a,i,t}$	Instantaneous fishing mortality rate for fish of age a in area i at year t
$F^{*}_{Y,a,i,t}$	Instantaneous fishing mortality rate for fish released in year Y in area i at year t for fish of age a
Fff_i	Degree of mixing of newly tagged fish in the release year in area i
M_a	Instantaneous natural mortality rate at age a
$Mini$	Tag-induced mortality rate in releasing tagged fish
$R_{c,i,t}$	Reporting rate by tag type c, area i, year t
$O_{b,d}$	Probability that a pop-up tag programmed to release in quarter b releases its stored data in quarter d
B	Relative pop-up probability of earlier quarters and a later quarter to the quarter of programmed pop-up date. These resultant pdfs are used for priors for $O_{b,d}$
W_c	Probability in a year that a tag does not shed or malfunction for tag type c in a quarter (c = 1) and a year (c = 2, 3)
$\varepsilon_{1,a,t}$	Process error deviation in survival for tag type 1, age group a, time step t
$\varepsilon_{c,a,i,t}$	Process error deviation in survival for tag type c (c = 2, 3), age group a, area i, time step t
$Reast$	Proportion of the archival tag reporting rate in the east in 2006 relative to the archival tag reporting rate in the west in 2006
$Rconv_{i,t}$	Proportion of the conventional tag reporting rate relative to the archival tag reporting rate in area i, year t
$H_{a,i,t}$	Harvest (exploitation) rate for fish of age a, area i, year t
$Rdrop_i$	Drop rate of archival tag reporting rate from 2005 to 2006 in area i

treated as a single population. Explanations for all symbols (indices, model variables, data, model parameters) used for this analysis are provided (Table 2).

Movement

For a fish of age a released in area i, there is a probability that it remains in its area i of residency for a three-month period (i.e., quarterly time step), $P_{a,i}$. If fish moving to another area j do not return within the year, the expected rate of transfer $T^{*}_{a,i,j,d}$ from area i to area j within d seasons of fish of age a is thus given by

$$(1) \qquad T^{*}_{a,i,j,d} = 1 - (P_{a,i})^{d}$$

The annual movement rate $T_{a,i,j}$ from area i to area j for fish of age a and the proportion staying in the same area i applied for archival and conventional tag models is also given by

$$(2) \quad T_{a,i,t} = T^{c}_{a,i,t,4}$$

$$(3) \quad T_{a,i,t} = 1 - T^{c}_{a,i,t,4}$$

Capture of pop-up tag data (tag type: c = 1)

For pop-up satellite tags, the quarter (d) in which the tag records are obtained is taken into account, such that the number of pop-up satellite tag reporting events is predicted separately for quarters 1 to 4. Satellite retrieval of data for pop-up satellite tags occurs within 9 months for all deployments. Therefore, a recapture model that accounts for a quarterly time step within each year is applied to the pop-up satellite tag data. The predicted number of pop-up satellite tags $C^{\varphi}_{1,Y,a,A,i,b,d}$ attached to fish of age a that successfully transmit stored data that were released in year Y in area A, reside in area i, after d quarters that were programmed to release in the bth quarter at liberty is given by

$$(4) \quad C^{\varphi}_{1,Y,a,A,i,b,d} = L^{\alpha}_{1,Y,a,A,b} \times T^{c}_{a,A,i,d} \times W^{d}_{1} \times O_{b,d} \times \varepsilon_{1,a,t}$$

where $L^{\alpha}_{1,Y,a,A,b}$ is the number of tags released in year Y in area A attached to fish of age a programmed to release in quarter b; W_1 is the probability that a tag does not shed or malfunction in a quarter; $O_{b,d}$ is the probability that a tag programmed to release in quarter b pops-off in quarter d; and $\varepsilon_{1,a,t}$ is a process error term depending on age a and yearly time t ($= Y + d/4$). The information available in the pop-up satellite tag records does not in all cases enable a verifiable elucidation of a pop-off event as a fishing mortality, natural mortality, or release from a live fish. Thus, modeling each of these events explicitly would make the estimation model more complicated without the data needed to support this. Instead, we introduced a slightly phenomenological parameter, $O_{b,d}$.

Catch and cohort equations for archival (c = 2) and conventional (c = 3) tag modeling

In the archival tag model, Fs from 1997 to 2006 are estimated, and in the conventional tag model, Fs from 1990 to 2006 are estimated. When year $t = Y$ (i.e., the year in which the tag group was released), the number of fish $N^{c}_{c,Y,a,A,i}$ carrying tag type c (2, archival tag; 3, conventional tag), of age a, released in year Y, in area A, moving to (or staying in) area i is given by

$$(5) \quad N^{c}_{c,Y,a,A,i,Y} = L^{\alpha}_{c,Y,a,A} \times (1 - Mini) \times T_{a,A,i} \times W_c$$

where $L^{\alpha}_{c,Y,a,A}$ is the number of tags released of tag type c in year Y in area A attached to fish of age a; $Mini$ is the tagging-induced mortality in releasing tagged fish; and W_c is the probability that a tag (type c) does not shed or malfunction in a year. When $t > Y$, this number of tagged fish is given by

$$(6) \quad N^{c}_{c,Y,a,A,i,t} = [N_{c,Y,a,A,i,t} \times T_{a,i,t} + N_{c,Y,a,A,i,t} \times T_{a,i,t}] \times W_c$$

where $N_{c,Y,a,A,i,t}$ is the number of fish carrying tag type c released in year Y in area A of age a and present in area i at year t.

The predicted number of tags $C^{\varphi}_{c,Y,a,A,i,t}$ of tag type c recovered from fish released in year Y in area A of age a, recaptured in area i in year t is given by

$$(7) \quad C^{\varphi}_{c,Y,a,A,i,t} = N^{c}_{c,Y,a,A,i,t} \times \frac{F^{c}_{Y,a,i,t}}{(M_a + F^{c}_{Y,a,i,t})} \times (1 - e^{-(M_a + F^{c}_{Y,a,i,t})}) \times R_{c,i,t}$$

where $F^{c}_{Y,a,i,t}$ denotes the instantaneous fishing mortality rate at age a for fish released in year Y recaptured in area i in year t; M_a is the instantaneous natural mortality rate at age a; and $R_{c,i,t}$ is the reporting rate of recaptured tags of type c in area i in year t. Hilborn (1990) utilized fishing effort data as a covariate to estimate Fs. This analysis, however, does not incorporate such information because there exist no long-term reliable effort data for Atlantic bluefin tuna fisheries. F for newly tagged fish is assumed to be lower in the first year than afterwards by a fraction Ffy, as the result of incomplete mixing, because the number of recaptures in the first year is significantly lower than expected. Thus, Ffy is less than 1.

$$(8) \quad F^{c}_{Y,a,i,t} = Ffy_i \times F_{a,i,t} \quad \text{for } t = Y$$

$$(9) \quad F^{c}_{Y,a,i,t} = F_{a,i,t} \quad \text{for } t > Y$$

where $F_{a,i,t}$ is the instantaneous fishing mortality rate at age a in area i in year t and Ffy_i is the degree of mixing of newly tagged fish in the release year in area i. The reporting rate for conventional tags is assumed to be lower than that of archival tags in each area.

$$(10) \quad R_{3,i,t} = Rcon_{i,t} \times R_{2,i,t}$$

where $Rcon_{i,t}$ denotes a proportion of the conventional tag reporting rate relative to the archival tag reporting rate in area i, year t. $Rcon_{i,t}$ is less than 1.

The update of the abundance of tagged fish between year t and year $t + 1$ is given by

$$(11) \quad N_{c,Y,a+1,A,i,t+1} = N^{c}_{c,Y,a,A,i,t} \times e^{-(M_a + F^{c}_{Y,a,i,t})} \times \varepsilon_{c,a,i,t}$$

where $\varepsilon_{c,a,i,t}$ is the process error deviation in survival for tag type c at age a in area i in year t.

Process error

Process errors represent deviations in state variables from model predictions in each time step. Relatively low prior variance is assigned to process error for the probability that a tag does not shed or malfunction (W) in the pop-up tag model and natural and fishing mortality rates (Z) in the archival and conventional models. The prior for standard deviation in process error is set at 2.5% per quarter for the pop-up satellite tag model and 10% per year for the archival and conventional tag models. The amount of process error for the pop-up satellite tag model depends on the period at liberty, e.g., tags that are at liberty for one quarter have larger process errors than those at liberty for three quarters. We could have added process error in different places in the archival and conventional tag models but doing so effectively increases the number of parameters estimated and adds to computational burden. We thus included one process error term at the end of the year (eq. 11) and chose to keep it separate from the observation error that was associated with eq. 7, which predicts the number of tags returned.

Table 3. Lists of prior pdfs and fixed default values used for this analysis.

Parameter	No. of parameters	Distribution	Source of origin
Pop-up tag model			
$P_{a,t}$	4	Beta(1, 1)	
$O_{b,d}$	14	Dirichlet	
B	1	Uniform(1, 2)	
W_1	1	Beta(1, 1)	
Archival tag model			
$T_{a,t,t}$	4	Beta	Posterior of pop-up tag model
M_a	1	Lognormal(0.14, 0.1^2)	Mean from assumption used for ICCAT stock assessment (2007)
$F_{a,t,t}$	36	Lognormal($F_{a,t,t}$, 0.8^2)	Mean from estimates by ICCAT stock assessment (2007)
Ffy_t	2	Beta(1, 1)	
W_2		0.95	
Mini		0.1	
$R_{2,t,t}$		0.7	
$R_{2,1,2006}$	1	Beta(1, 1)	
Reast	1	Beta(1, 1)	
Conventional tag model			
$T_{a,t,t}$	6	Beta	(ages 0–3) posterior of archival tag model for ages 4–8 (ages 4–8 and 9+) posterior of archival tag model
M_a	1	Lognormal	Posterior of archival tag model
$F_{a,t,t}$	96	Lognormal	(ages 0–3) mean from estimates during 1990–2006 by ICCAT stock assessment (2007) (the variance is 0.8^2) (ages 4–8 and 9+) posterior of archival tag model during 1997–2006. Mean from estimates during 1990–1996 by ICCAT stock assessment (2007) (the variance is 0.8^2)
Ffy_t	2	Beta	Posterior of archival tag model
$Rcon_{t,t}$	4	Beta(1, 1)	
W_3		0.95	
Mini		0.1	

A symmetric uniform distribution around 1 is proposed for the process error in survival rates. Michielsens et al. (2006) found that a uniform density function is computationally more efficient than permutations of lognormal process error terms. This specification for the process error intervals is sensible, provided that it does not permit the number of tags to increase between time steps, i.e., in the case of archival and conventional tag models, the product of the total survival rate e^{-Z} and the process error should be smaller than 1. Therefore, the process error in each year will be estimated in a range larger than 0 and smaller than e^Z as an additional constraint.

Observation model

Observation error is modeled using a negative binomial distribution as a general form. For simplicity in terms of model stability and computational burden, the Poisson distribution is used in this analysis. The Poisson distribution is an extreme form of negative binomial distribution; the observation error variance equals the model prediction for returned tag numbers.

$$(12)\quad C^{o}_{c,Y,a,l,i,d} \sim \text{Poisson}(C^{e}_{c,Y,a,l,i,d}) \quad \text{for } c = 1$$

$$(13)\quad C^{o}_{c,Y,a,l,i} \sim \text{Poisson}(C^{e}_{c,Y,a,l,i}) \quad \text{for } c = 2, 3$$

Prior probability density function (pdf)

Prior pdfs of estimated parameters were set for the base-case scenario as follows (Table 3). Furthermore, for some parameters, alternative specifications for priors were examined as sensitivity tests, which are described below.

Pop-up satellite tag model

In the current analysis, a non-informative prior pdf, Beta(1, 1), is used for age-specific movement rates. This prior represents a uniform distribution between 0 and 1. The fraction of tags within a quarter that do not fail or shed, W_1 is also estimated using the non-informative prior pdf. Many pop-up satellite tags release prior to their programmed release time. Attachment failure has many sources but includes pin breakage, nose-cone failure, tether wearing, dart dislodging, natural mortality, and predators biting off the tags. Thus, the recovery chance of information $O_{b,d}$ is presumed to be nonzero in all quarters before the planned quarter of detachment but nonzero only for one quarter after its programmed date. The Dirichlet distribution is assumed as the prior pdfs. The prior expectation for pop-up satellite tag recovery is the highest in the quarter of programmed date and $1/B$ times as likely in each earlier quarter and a later quarter, where B is a hyperparameter of the Dirichlet distribution. For example, when $B = 2$ and the tag detach-

ment is programmed in the third quarter, a relative pop-up probability is 0.111, 0.222, 0.444, and 0.222 in the first, second, third, and fourth quarters, respectively. B is an estimated parameter. The prior pdf of B is Uniform(1, 2).

Archival tag model

Stock assessment for Atlantic bluefin tuna is conducted by ICCAT using a VPA-type model (ICCAT 2007). The ICCAT assessment has a different assumption on the movement from our model (no transoceanic migration), and growing evidence suggests that this assumption is not appropriate (e.g., Block et al. 2001, 2005). This does not imply that ICCAT's assessment results are biased, because ICCAT's model explains a variety of fishery-related data such as catch per unit effort (CPUE). Thus, the fishing mortality rate estimate, depending on age and year, is used as a mean value of the prior, and a moderately high prior variance value (0.8^2 on the log scale) was applied. This prior setting permits the new data and model structure to update the prior. "Run3" results for the east area and "base case" results for the west area are used (ICCAT 2007). "Run3" is one of three scenarios examined in the 2006 ICCAT assessment and the results of it were investigated in detail. The mean value for M was the same as that utilized for the western management unit fish in the ICCAT stock assessment (2007), i.e., 0.14·year^{-1}. A relatively small variance (0.1^2 on the log scale) was applied, as M is generally not treated as a highly uncertain parameter. There is no information on the degree of incomplete mixing of newly tagged fish (Ffy). Therefore, the noninformative prior, Beta(1, 1), is applied. The initial tag-induced mortality rate, $Mini$, was assumed to be 0.1·year^{-1}. This value was arbitrarily set but did not impact greatly final results because the effect was countered by the Ffy estimate. The probability that a tag does not shed or malfunction in a year, W, was set at 0.95, which led to almost the lowest deviance information criterion (DIC). Preliminarily, sensitivity analyses showed that varying this value over realistic ranges did not influence the general results.

The posterior pdf of movement rates in the pop-up satellite tag model, approximated by the beta distribution, is used for the prior in the archival tag model. In general, the approximation was reasonably good, and complicated posteriors such as bimodal distributions were not observed. Prior correlations between parameters in the archival tag model are not considered, because posterior correlations in the pop-up satellite tag model are less than 0.01. Movement rates from east to west estimated from pop-up satellite tags attached to eastern management unit (the Mediterranean Sea) fish are applied to east-to-west movements of western management unit fish in the base-case scenario, because no other information exists and no stock structure is assumed in the present analysis.

Conventional tag model

For common parameters between the archival and conventional tag models, such as fishing mortality rates, movement rates, and mixing rates of newly tagged fish (Ffy), posterior distributions of the archival tag model are used as priors of the conventional tag model. Parameters in the interval (0, 1) are modeled using the beta distribution; other parameters are represented by the lognormal distribution. None of the posterior distributions obtained from the archival tag model deviated noticeably from these two distributions. Prior correlations between parameters in the conventional tag model are not considered because posterior correlations in the archival tag model are generally small and the highest value is about 0.4.

In terms of model structure, the conventional tag model expands the archival tag model to include younger fish (ages 0–3) and more years (1990–1996). Thus, new priors for F and movement rates are described (Table 3).

Base-case scenario and sensitivity analysis

Base-case scenario

The following assumptions are incorporated for the base-case scenario set as a standard basis for examining model sensitivity to different assumptions. Thus, it is not to say that the base-case results are the most plausible. (*i*) Age-specific movement rates and fishing mortality rates apply to three age groups: ages 0–3, ages 4–8, and ages 9+. A two-age-group model (ages 0–8 and ages 9+) was also examined. The goodness of fit of this model to the data, however, was much worse than that of the three-age-group model. In this study, archival and pop-up satellite tags were only attached to fish over age 4. Thus, parameters for ages 0–3 were estimated from conventional tag data only. (*ii*) Archival tag reporting rates during 1997–2005 were fixed at 0.7 in both areas. On the other hand, the 2006 reporting rate was estimated so as to satisfy the condition that F in 2005 was equal to F in 2006. Additionally, the eastern reporting rate was assumed to be lower than the western rate by a fraction $Reast$.

$$R_{2,2,2006} = Reast \times R_{2,1,2006} \quad (14)$$

The prior for $R_{2,1,2006}$ and $Reast$ was set as Beta(1, 1). This constraint comes from an expert judgment based on recent differences in campaign activity for tag returns between the west and the east. It also helps to avoid possible overparameterization. (*iii*) Conventional tag reporting rates were modeled to depend on area (west and east) and time period (1990–1998, 1999–2005). This assumption that reporting rate is constant over a period of years facilitates the estimation of fishing mortality rates. For both time periods, reporting rates were assumed to be less than that for archival tags (0.7), although archival tag data were not available before 1997. The 2006 reporting rate is assumed to drop from the 2005 rate to the same degree as the drop of the archival tag reporting rate from 2005 to 2006 in area i ($Rdrop_i$) to avoid possible overparameterization. (*iv*) Fishing mortality rates in 2006 were assumed to be the same as those in 2005, because the number of tag returns in 2006 is not yet finalized.

Sensitivity analysis

Some sensitivity analyses are conducted to test the sensitivity of estimates of parameters to model assumptions (Table 4). In estimating fishing mortality rates from tagging data, one of the largest uncertainty sources is the reporting rate estimate (Martell and Walters 2002). Currently, no reliable auxiliary data, such as observer data, are available to estimate reporting rates by areas or fleets. Therefore, sensi-

Table 4. Sensitivity analysis specifications.

Scenario	Archival tag model	Conventional tag model
1	Base case: $F_{a,1,2005} = F_{a,1,2006}$, $R_{2,1,1997\text{–}2005} = R_{2,2,1997\text{–}2005} = 0.7$, $R_{2,1,2006} \geq R_{2,2,2006}$: estimation	Base case: see the section Base-case scenario
1*b*	Base case	$R_{3,1,2006}$, $R_{3,2,2006}$: estimation independent of *Rdrop*
1*c*	Base case	$R_{3,1,1999\text{–}1998} = R_{3,1,1999\text{–}2005}$, $R_{3,2,1999\text{–}1998} = R_{3,2,1999\text{–}2005}$
2	$R_{2,1,1997\text{–}2005} = R_{2,2,1997\text{–}2005} = 0.3$	Base case
3	$R_{2,1,1997\text{–}2005} = R_{2,2,1997\text{–}2005} = 0.9$	Base case
4	$R_{2,1,1997\text{–}2005} = 0.7$, $R_{2,2,1997\text{–}2005} = 0.3$	Base case
5	$R_{2,1,1997\text{–}2005} = 0.3$, $R_{2,2,1997\text{–}2005} = 0.7$	Base case
6	$R_{2,1,2006} = R_{2,2,2006}$	$R_{3,1,1999\text{–}1998} = R_{3,2,1999\text{–}1998}$, $R_{3,1,1999\text{–}2005} = R_{3,2,1999\text{–}2005}$, $R_{3,1,2006} = R_{3,2,2006}$
7	$R_{2,1,1997\text{–}2005}$, $R_{2,2,1997\text{–}2005}$: estimation ($R_{2,1,1997\text{–}2005} \geq R_{2,2,1997\text{–}2005}$)	Base case
8	$R_{2,1,2006} = R_{2,2,2006} = 0.7$, $F_{a,1,2005} \neq F_{a,1,2006}$	$R_{3,1,2006} = R_{3,1,1999\text{–}2005}$, $R_{3,2,2006} = R_{3,2,1999\text{–}2005}$, $F_{a,1,2005} \neq F_{a,1,2006}$
9	Non-informative prior for harvest rate	Base case
10	Base case	$W_3 = 0.85$
11	Age-specific M_a	Age-specific M_a
12	Less informative prior for M_a	Base case
13	Drop tag return data in 2006	Drop tag return data in 2006
14	Negative binomial likelihood	Negative binomial likelihood

tivity tests were conducted to cover a range of possible reporting rate assumptions (scenarios 1–8).

A less informative prior for fishing mortality rates was examined (scenario 9). The fishing mortality rate can be formulated using the harvest (exploitation) rate, H:

$$(15) \qquad F_{a,i,j} = -\ln(1 - H_{a,i,j})$$

The prior pdfs of the harvest rates were given by Beta(1.2, 1.2). This prior represents that harvest rates have high uncertainty between 0 and 1, but the probability that harvest rates are near 0 or 1 is lower.

Hampton and Kirkwood (1990) indicated that tag-shedding rates of southern bluefin tuna might be higher than our base-case assumption (0.05). Thus, a lower value of W_3 (not-shedding rate; 0.85) was examined (scenario 10). Different natural mortality assumptions were examined. Age-specific mortality rates ($M_1 = 0.323$, $M_2 = 0.201$, and $M_3 = 0.113$ for ages 0–3, ages 4–8, and ages 9+, respectively), which were averaged for each age group used for the eastern area in ICCAT (ICCAT 2007), were applied for both areas (scenario 11). A less precise prior on M (0.8^2 on the log scale) was also examined, particularly to examine influences on the estimation of F (scenario 12). In the base-case scenario, some assumptions were applied to estimate Fs for 2006 because the number of tag returns in 2006 was not finalized. To examine influences of these assumptions, the archival and conventional tag return data for 2006 were left out and all parameters were estimated until 2005 (scenario 13).

To consider the possibility of overdispersion in tag returns, returns of the three tag types were assumed to be distributed according to a negative binomial distribution (scenario 14). We used the probability density of the following form (Hilborn and Mangel 1997):

$$(16) \qquad p(C^o|\theta) = \frac{\Gamma(k + C^o)}{\Gamma(k)C^o!}\left(\frac{k}{k + C^p}\right)^k\left(\frac{C^p}{C^p + k}\right)^{C^o}$$

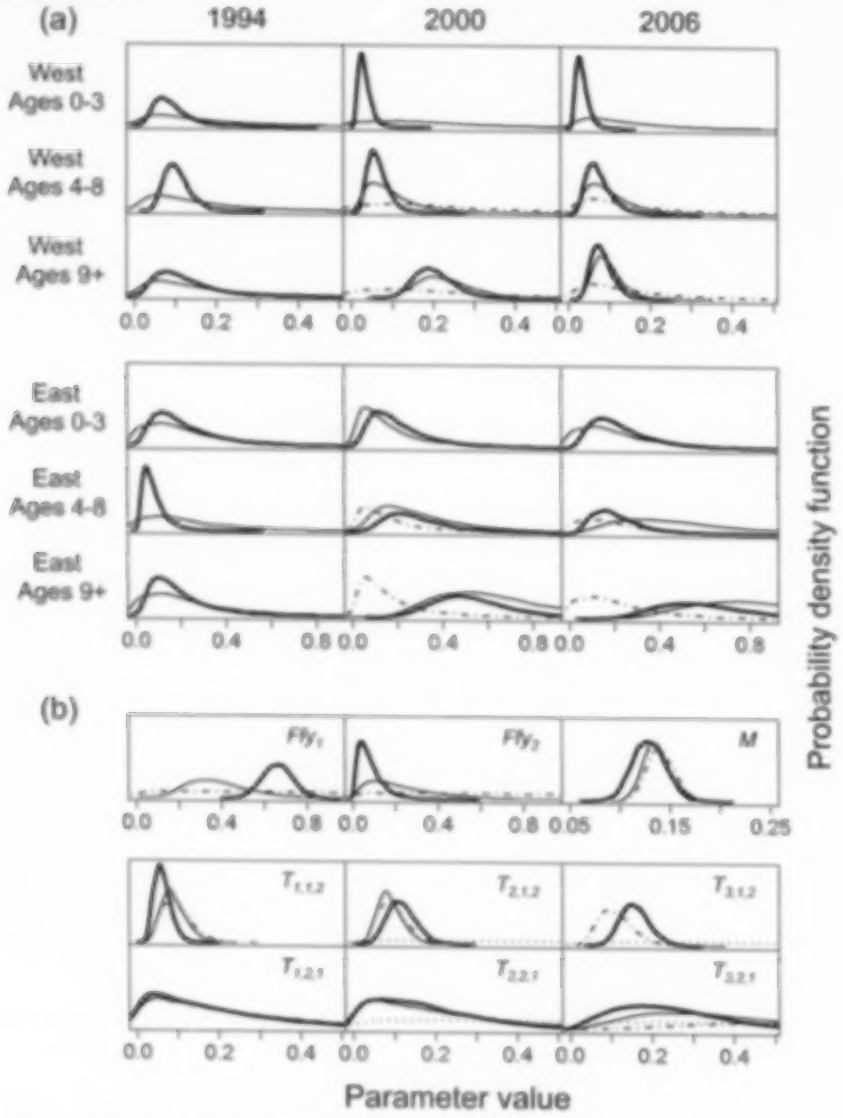
where Γ denotes the gamma function, θ represents a particular set of parameters, C^o and C^p represent the observed and predicted number of tag returns, respectively, and k is the overdispersion parameter. In this case, the variance in C^o given θ is $m + m^2/k$, where m represents C^p. k was assumed to be common for all data, and the prior was set as Uniform(0.1, 10) to cover moderately wide ranges.

MCMC (Markov chain Monte Carlo) modeling diagnostics

This Bayesian analysis was implemented using WINBUGS software, which has been applied successfully to mark–recapture problems similar in complexity (Michielsens et al. 2006). The comparative model fit was evaluated by DIC used for Bayesian models (Spiegelhalter et al. 2002). When the difference in DIC between models was more than 3–7, they were regarded to be "importantly" different as a rule of thumb (Spiegelhalter et al. 2002). In addition, the fit of the model to the data was assessed by comparing each data point with its posterior predictive distribution. Bayesian p values for observations are defined as the probability that a model-predicted data point is greater than the observed data point (Meng 1994).

Convergence diagnostics have been applied to obtain numerically stable posterior estimates. The main ones examined include the Gelman–Rubin–Brooks (BGR) plot (Best et

Fig. 2. Prior and posterior distributions of (*a*) fishing mortality rates and (*b*) other parameters (dotted line, pop-up tag model prior; dotted–dashed line, archival tag model prior; solid line, conventional tag model prior; bold solid line, conventional tag model posterior). Subscripts of parameters are defined in Table 2.



al. 1997), Monte Carlo (MC) error (standard error of the mean of the sampled values), and the comparison of the posterior distribution between the first 10% of each chain and the last 10%. The BGR plot shows the ratio of variability of the pooled chains to average variability within each chain; it should be horizontal and converge on the value of 1.0. MC error should be less than 5% of the estimated posterior SD (Gilks et al. 1995). "Burn-in" (discarding some of the initial samples from a chain; Gelman et al. 2004) was conducted to provide samples independent of initial values. Thinning (retaining simulation draws at a fixed interval and discarding the rest) was not conducted because of the low autocorrelation of Markov chains. Convergence diagnostics showed that MCMC chains had converged quickly. Therefore, the number of chains, sampling iterations, and the length of burn-in were regarded as reasonable (for detailed information, see Supplementary material available online from the NRC Data Depository).[3] It was assumed that the reported posteri-

[3] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3880. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

Table 5. Summary results for the base-case scenario.

Parameter	Age	Area	Mean (SD)	10%	50%	90%
Average fishing mortality (t: 1990–2006)						
$F_{1,1,t}$	0–3	West	0.082 (0.012)	0.067	0.081	0.098
$F_{2,1,t}$	4–8	West	0.111 (0.014)	0.094	0.111	0.130
$F_{3,1,t}$	9+	West	0.167 (0.029)	0.135	0.163	0.203
$F_{1,2,t}$	0–3	East	0.364 (0.092)	0.262	0.350	0.481
$F_{2,2,t}$	4–8	East	0.180 (0.036)	0.138	0.175	0.226
$F_{3,2,t}$	9+	East	0.330 (0.055)	0.265	0.325	0.403
Reporting rate						
$R_{3,1,1990\text{–}1998}$		West	0.232 (0.037)	0.188	0.229	0.281
$R_{3,1,1999\text{–}2005}$		West	0.112 (0.019)	0.088	0.110	0.137
$R_{3,1,2006}$		West	0.057 (0.010)	0.045	0.056	0.070
$R_{3,2,1990\text{–}1998}$		East	0.136 (0.042)	0.088	0.129	0.191
$R_{3,2,1999\text{–}2005}$		East	0.064 (0.019)	0.043	0.061	0.089
$R_{3,2,2006}$		East	0.023 (0.007)	0.015	0.022	0.031
Movement rate						
$T_{1,1,2}$	0–3	West to east	0.062 (0.020)	0.038	0.060	0.089
$T_{2,1,2}$	4–8	West to east	0.118 (0.035)	0.075	0.116	0.165
$T_{3,1,2}$	9+	West to east	0.159 (0.036)	0.114	0.156	0.206
$T_{1,2,1}$	0–3	East to west	0.185 (0.158)	0.023	0.142	0.412
$T_{2,2,1}$	4–8	East to west	0.184 (0.140)	0.031	0.154	0.378
$T_{3,2,1}$	9+	East to west	0.258 (0.149)	0.086	0.234	0.463
Degree of mixing						
Ffy_1		West	0.661 (0.071)	0.570	0.661	0.753
Ffy_2		East	0.079 (0.060)	0.020	0.064	0.157
Natural mortality						
M			0.136 (0.012)	0.121	0.136	0.152

Note: Subscripts of parameters are described in Table 2.

ors were representative of the underlying stationary distributions.

Results

Bayesian parameter update in the sequential analysis

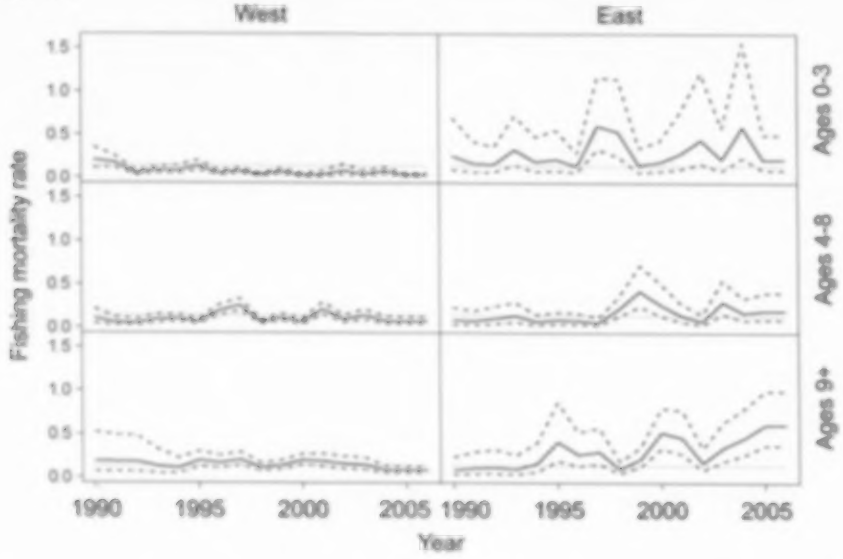
Most of the parameter estimates were updated successively throughout the sequential analysis and with the increases in information considered (Fig. 2). Fishing mortality rates (Fs) were estimated more precisely than the original prior for the archival tag model, indicating that archival and conventional tag data together can provide useful information about Fs. In particular, recent Fs for ages 4–8 and 9+ in the west were substantially updated because there were plenty of tags of both types placed on these age groups. The estimation of western Fs at ages 0–3 was improved because of the numerous conventional tag releases included in this analysis. Generally, F estimates in the east or in the early period had large uncertainties due to fewer tag releases. In some cases (e.g., eastern F for ages 4–8 in 1994), however, tagging data, especially conventional, made Fs more informative in the current analysis.

Final posteriors for movement rates (T) were more precise than non-informative priors (Fig. 2) when using results from the pop-up satellite tag model, particularly for west to east movement, partly because there are many pop-up satellite tag recoveries. They were slightly updated afterwards through archival and conventional tag models. Mixing rates of fish tagged and fish targeted by fisheries in the release year (Ffy) indicated different features between the two areas, which might reflect differences in the spatiotemporal matching among age-specific fish behaviors, fishing operations, and tag deployment places (Fig. 2). In the west, the posterior means for mixing rate parameters (Ffy) in the conventional tag model were considerably higher than the prior means, i.e., based on the posterior obtained from the archival tag model. On the other hand, the final estimate in the east was very low. The M estimate showed almost the same posterior density distribution as that of the prior, as the prior precision was set high. Summary results for the base case of the pop-up satellite tag model and the archival tag model are provided (Appendix A, Tables A1 and A2 and Fig. A1).

Results for the base-case scenario

Average F estimates between 1990 and 2006 for the three age groups were on the order of 0.08 (standard deviation, SD = 0.01) (ages 0–3) to 0.17 (SD = 0.03) (ages 9+) in the west (Table 5). F estimates for juvenile fish showed no increasing or decreasing trends from 1990 to the present (Fig. 3). Although F estimates of ages 0–3 were relatively low, the 80% probability intervals for F for ages 4–8 and 9+ overlapped with that for M. The F estimates for western fish were more precise than those for eastern fish, as more data were available for these age groups. Average Fs were from 0.18 (SD = 0.04) (ages 4–8) to 0.36 (SD = 0.09) (ages 0–3) in the east (Table 5; Fig. 3). They were about 60%–340% higher than those of the west. In the east, Fs for ages 4–8 and 9+ have increased since the late 1990s, although

Fig. 3. Posterior distribution of fishing mortality rates of each age group and area from the conventional tag modeling. Solid line represents the posterior median. Broken lines represent the 10th and 90th percentiles of the posterior. The dotted line represents the posterior median of the natural mortality rate.



uncertainty in the estimates was relatively high because of a small number of returns.

Estimates of conventional tag reporting rates after 1999 were 0.11 (SD = 0.02) in the west and 0.06 (SD = 0.02) in the east (Table 5). They were about half of those in the early time in both areas (0.23 (SD = 0.04) in the west and 0.14 (SD = 0.04) in the east). This reporting rate drop led to higher F estimates.

The estimates of movement rates from the west to east were mostly consistent with general conclusions of Block et al. (2005) about crossover rates depending on size, i.e., crossover rates are higher for larger fish (Table 5). Annual movement rate estimates (west to east) varied from 6.2% (SD = 2.0%) for fish of ages 0–3 to 11.8% (SD = 3.5%) for fish of ages 4–8 and 15.9% (SD = 3.6%) for fish of ages 9+. The estimates of east-to-west movement rates were much less precise than the west-to-east movement rates: 18.5% (SD = 15.8%) at ages 0–3, 18.4% (SD = 14.0%) at ages 4–8, and 25.8% (SD = 14.9%) at ages 9+.

The goodness of fit of the model to the observed data appeared to be acceptable (Fig. 4). Many of the observed data were included within 10% to 90% of the estimated posterior distribution. In general, posterior correlations between estimates were low. This indicates that parameters can be estimated without confounding. Movement rates, reporting rates, and fishing mortality rates show some correlation, although the correlation was <0.5.

Sensitivity analysis results

The estimated F in 2005 and 2006 was slightly lower when conventional tag reporting rates in 2006 were estimated, independent of the drop rate of archival tag reporting rates (scenario 1*b*). The differences, however, were small (e.g., $F_{2.1,2006}$ = 0.072 (SD = 0.032) for scenario 1*b*, 0.076 (SD = 0.033) for the base case). Under the assumption that reporting rates did not change over time, F estimates in the early period were higher than the base case, but those in the recent period were lower than the base case (scenario 1*c*; Fig. 5*a*). The goodness of fit of the model, however, was worse (Table 6).

With higher fixed values for archival tag reporting rates, Fs estimated from conventional tag modeling were generally lower (scenarios 2 and 3; Table 6; Fig. 5*b*). These differences, however, were not statistically significant, i.e., 95 percentiles of probability distributions of parameter estimates overlapped. DIC also showed that the goodness of fit was not different among these scenarios. Moreover, the presumed differences in archival tag reporting rate between areas did not significantly impact F estimates, although reporting rates and movement rates changed slightly (scenarios 4 and 5; Table 6). When the same reporting rates were applied to both areas (scenario 6), movement rates were different from those for the base-case scenario, but not significantly so. F estimates were identical. When archival tag reporting rates were estimated (0.74 in the west and 0.62 in the east; scenario 7; also see Appendix A, Table A2), these estimates did not significantly impact the final results of the conventional tag model. Ignoring the high uncertainty in tag return numbers in 2006 and assuming the same reporting rate in 2006 as that in 2005 (scenario 8), Fs in 2006 dropped as expected (e.g., $F_{2.1,2006}$ = 0.058 (SD = 0.034)). These results for scenarios 2 to 8, in addition to scenario 1, indicate that time trends of Fs are considerably robust to uncertainties in archival tag reporting rates. Another characteristic was that only a small number of specific parameters did not change significantly. Rather, many parameters were changed slightly at the same time.

The alternative F priors did not have a large impact on recent F estimates in the west (scenario 9; Table 6;

Fig. 4. Observed (○) and predicted (lines) distribution of the number of conventional tag returns released from 1995 to 1998, when many tags were released. The solid line represents the posterior median of expected number of tag returns. Broken lines represent the 10th and 90th percentiles of the posterior.

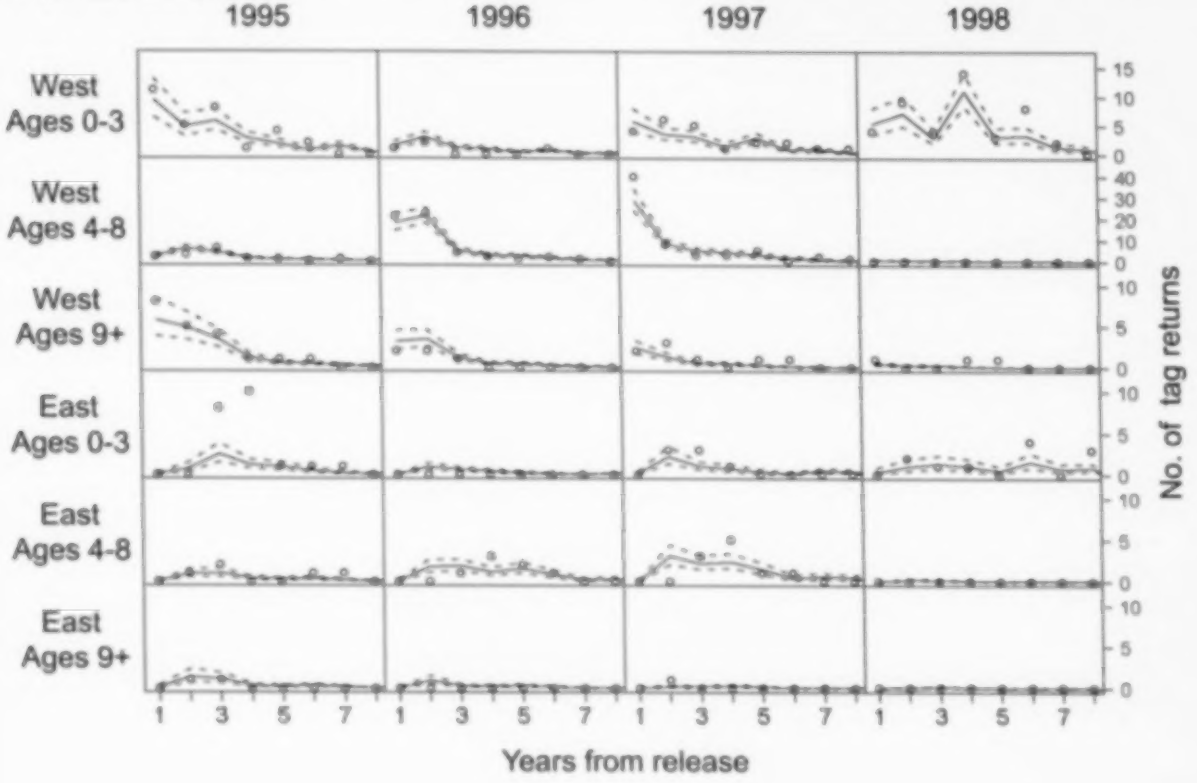


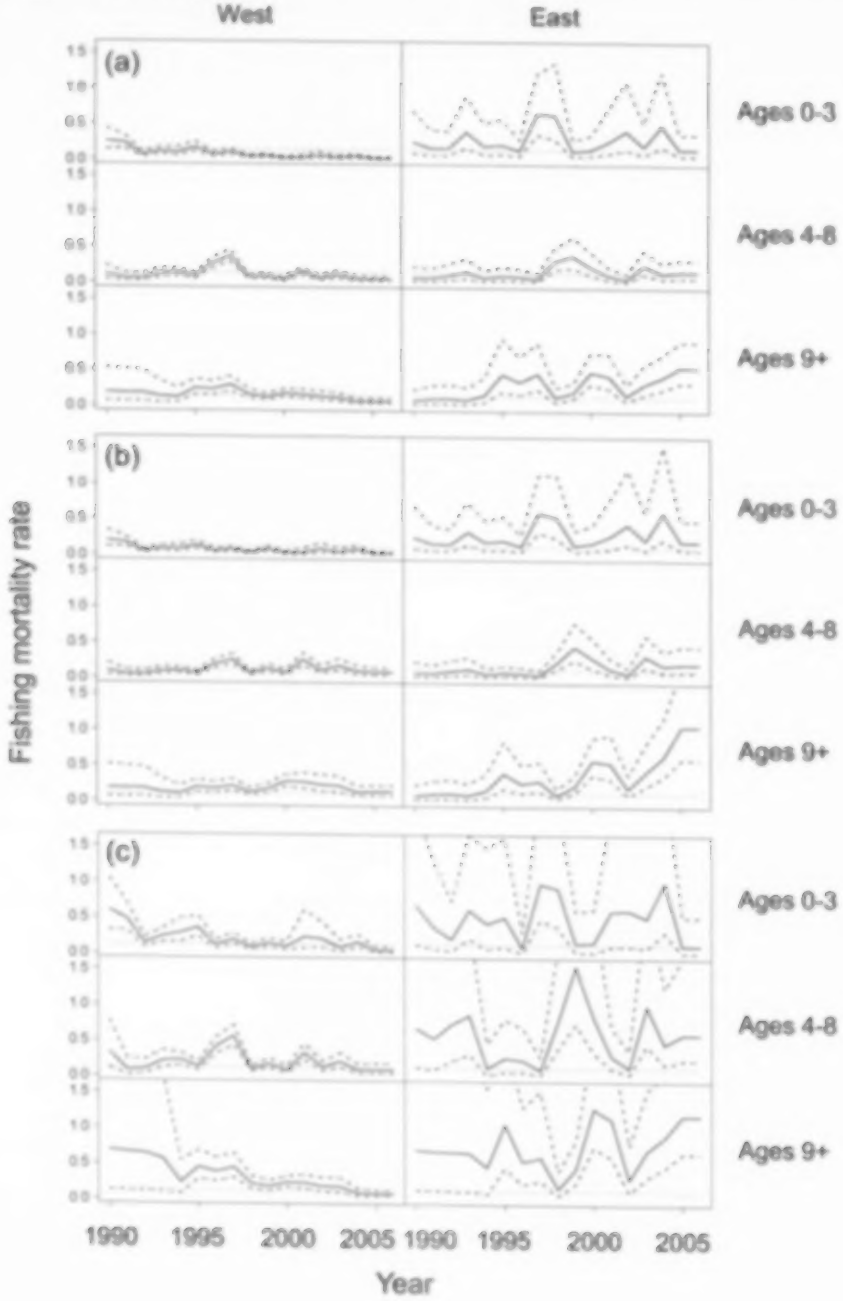
Fig. 5c). This indicates that the tagging data updated prior information considerably. On the other hand, priors for F significantly influenced results for ages 4–8 and 9+ in the east, and the estimates were only moderately updated due to relatively sparse data. The higher tag shedding rate gave poor fits to the data (scenario 10). Although this assumption estimated higher reporting rates, F estimates were not significantly different. Age-specific natural mortality rates did not impact Fs and movement rates (scenario 11). DIC did not support this assumption of age-specific Ms. When the less informative M prior was used, the final M estimate had larger variance (M = 0.118 (SD = 0.031); scenario 12). Correlations with Fs were still low, although moderately high correlations (about 0.4) with reporting rates were observed. Incorporation of the 2006 data often led to slightly lower Fs in 2005, e.g., F for ages 9+ in the west was 0.094 (SD = 0.033) in scenario 13, whereas in the base case, F was 0.084 (SD = 0.028). Exclusion of the 2006 data did not impact other parameters. When considering overdispersion with negative binominal likelihood, the pop-up tag model showed a much better fit to the data and movement rates had slightly larger uncertainty (scenario 14; Appendix A, Table A1). In the archival and conventional tag models, however, parameter estimates were not significantly different, and the model fit to the data was almost same.

Discussion

Advantages of Bayesian approach to integrate multiple tagging data

Bayesian state–space models can evaluate parameter uncertainties based on the amount of information available by accounting for process and observation errors explicitly (Millar and Meyer 2000; Punt 2003; Michielsens et al. 2006). Bayesian methods also provide a statistically rigorous framework with which to integrate various data sources and knowledge sequentially, following the main concept of Bayesian inference, i.e., that information is updated with new data. In this framework, parameters of interest can be estimated in a conceptually consistent and computationally feasible manner, with a single estimation model formulated for each major component of the estimation problem, although this study requires that posterior distributions can be approximated by parametric distributions. The updating of posterior pdfs as shown herein indicates that the sequential approach functions well in the estimation of fishing mortality and movement rates by combining data from three different types of tags. Michielsens et al. (2008) applied the sequential approach to the stock assessment for Baltic salmon. They estimated stock abundance trends by combining a wide range of results and information from other analyses,

Fig. 5. Posterior distribution of fishing mortality rates of each age group and area for (*a*) scenario 1c, (*b*) scenario 2, and (*c*) scenario 9. The solid line represents the posterior median. Broken lines represent the 10th and 90th percentiles of the posterior. The dotted line represents the posterior median of the natural mortality rate.



such as stock–recruit relationship, exploitation rates, and natural mortality. In general, each data source used for stock assessment is sparse. Therefore, it is important to synthesize many kinds of data to better understand the stock status (Punt and Hilborn 1997). Bayesian sequential estimation provides a rigorous methodology for such situations.

The present tagging models also show that there is a synergy in combining fishery-independent tag information (e.g.,

Table 6. Summary results of sensitivity tests (mean values of parameter estimates).

			Scenario													
	Age	Area	1*b*	1*c*	2	3	4	5	6	7	8	9	10	11	12	13	14
DIC			1615.6	1624.1	1616.1	1614.9	1614.0	1617.0	1614.5	1614.8	1617.1	1629.5	1622.8	1629.9	1614.7	1564.6	1617.5
n			111	107	109	109	109	109	107	109	115	109	109	111	109	109	110
Parameter																	
Average fishing mortality (*t*: 1990–2006)																	
$F_{1,t}$	0–3	West	0.081	0.092	0.085	0.080	0.079	0.086	0.089	0.080	0.083	0.222	0.073	0.080	0.083	0.086	0.086
$F_{2,t}$	4–8	West	0.111	0.119	0.127	0.105	0.111	0.128	0.119	0.110	0.114	0.211	0.105	0.115	0.111	0.117	0.109
$F_{3,t}$	9+	West	0.166	0.180	0.206	0.156	0.170	0.204	0.174	0.166	0.168	0.394	0.163	0.162	0.164	0.172	0.170
$F_{1,t}$	0–3	East	0.364	0.358	0.365	0.364	0.362	0.370	0.358	0.363	0.385	0.656	0.361	0.370	0.366	0.368	0.379
$F_{2,t}$	4–8	East	0.178	0.178	0.195	0.175	0.189	0.184	0.175	0.181	0.180	0.790	0.180	0.188	0.178	0.181	0.179
$F_{3,t}$	9+	East	0.327	0.342	0.427	0.308	0.400	0.351	0.313	0.341	0.316	0.919	0.325	0.324	0.323	0.310	0.339
Reporting rate																	
$R_{1,1,1990–1996}$		West	0.234	0.169	0.215	0.240	0.251	0.203	0.199	0.239	0.234	0.117	0.308	0.273	0.221	0.233	0.238
$R_{1,1,1997–2005}$		West	0.111	0.169	0.091	0.121	0.122	0.084	0.093	0.116	0.104	0.073	0.161	0.133	0.109	0.110	0.109
$R_{1,1,2006}$		West	0.101	0.086	0.074	0.055	0.053	0.077	0.040	0.055	0.104	0.035	0.082	0.068	0.053	0.056	0.056
$R_{1,2,1990–1996}$		East	0.139	0.081	0.115	0.148	0.099	0.154	0.199	0.126	0.141	0.156	0.210	0.161	0.130	0.136	0.125
$R_{1,2,1997–2005}$		East	0.065	0.081	0.052	0.071	0.044	0.075	0.093	0.059	0.062	0.095	0.112	0.078	0.062	0.063	0.063
$R_{1,2,2006}$		East	0.069	0.029	0.029	0.023	0.028	0.022	0.040	0.023	0.062	0.032	0.040	0.028	0.021	0.022	0.022
Movement rate																	
$T_{1,1,2}$	0–3	West to east	0.061	0.072	0.070	0.058	0.083	0.053	0.045	0.066	0.058	0.042	0.051	0.060	0.063	0.064	0.064
$T_{2,1,2}$	4–8	West to east	0.118	0.124	0.127	0.112	0.152	0.104	0.091	0.127	0.119	0.055	0.109	0.121	0.119	0.120	0.129
$T_{3,1,2}$	9+	West to east	0.156	0.164	0.183	0.149	0.196	0.149	0.142	0.165	0.154	0.132	0.154	0.157	0.156	0.156	0.164
$T_{1,2,1}$	0–3	East to west	0.190	0.166	0.181	0.187	0.164	0.201	0.220	0.181	0.195	0.202	0.212	0.190	0.184	0.187	0.205
$T_{2,2,1}$	4–8	East to west	0.194	0.167	0.180	0.192	0.149	0.225	0.286	0.181	0.195	0.445	0.242	0.207	0.181	0.190	0.220
$T_{3,2,1}$	9+	East to west	0.265	0.233	0.243	0.275	0.195	0.303	0.401	0.241	0.261	0.672	0.308	0.262	0.266	0.275	0.259
Degree of mixing																	
Ffy_1		West	0.661	0.667	0.730	0.636	0.041	0.748	0.688	0.658	0.659	0.530	0.602	0.609	0.677	0.645	0.646
Ffy_2		East	0.078	0.087	0.088	0.075	0.086	0.078	0.070	0.081	0.080	0.042	0.065	0.070	0.081	0.077	0.079
Natural mortality																	
M			0.137	0.138	0.121	0.141	0.129	0.127	0.137	0.136	0.138	0.126	0.128		0.118	0.136	0.136
M_1														0.268			
M_2														0.195			
M_3														0.116			
Overdispersion																	
k																	4.868

Note: DIC, deviance information criterion; *n*, number of parameters. For the base case, DIC = 1614.8 and *n* = 109. The number of parameters represents all except process error terms. Standard deviations are shown in the Supplementary material (available online from NRC Data Depository).

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pop-up satellite tag) with fishery-dependent tag information (e.g., archival and conventional tags). There have been numerous examples of quantitative models using tagging data to estimate parameters regarding population dynamics such as stock size, natural mortality, exploitation rates, reporting rates, and movement rates (Quinn and Deriso 1999; Walters and Martell 2004). These factors, however, tend to be confounded and it is often difficult to solve this issue. To overcome this issue, some studies have used other additional information in tagging data analyses but very few studies have applied the Bayesian approach. Polacheck et al. (2006) demonstrated that incorporation of catch-at-age data into tag-recapture analysis improves mortality estimation. Radiotelemetry information also provides more precise and unbiased mortality estimates, including reporting rate estimates (Nasution et al. 2001; Pollock et al. 2004).

It is important to note that the three kinds of tagging data in this study provided complementary information for the estimation of *F*s and movement rates to understand the entire life history of the bluefin tuna and fishery stock management. When pop-up satellite tag information was not used, statistically valid estimates could not be obtained, as movement rates had higher uncertainty and higher correlations between themselves and *F*s. This shows that pop-up satellite tag data are critical to estimating *F*s, as well as movement rates, while not providing information on *F*s themselves. Also archival and conventional tags cover different age ranges of fish tagged, which is important for estimating age-specific (size-specific) *F*s over a wider range of ages. *F* estimates for ages 9+ have larger uncertainty in the earlier 1990s compared with the later 1990s, as archival tag data were not available for the earlier time periods.

Thus far, few methodologies have been developed to estimate both movement and fishing mortality rates (Sibert et al. 1999; Hampton and Fournier 2001; McGarvey and Feenstra 2002). Fishery-independent, as well as fishery-dependent, tagging data would be useful to reduce uncertainties for movement rates, but such tagging research is still rare because of high deployment costs. The present study capitalized on the highest number of pop-up satellite tagging records yet available for fisheries analysis. Moreover, Bayesian tagging models have shown improved performance over maximum likelihood approaches, even in such cases where tagging data are relatively sparse (Chao 1989; Martell and Walters 2002). This is partly a result of incorporating additional information as a prior density function. These two factors make it possible to estimate exploitation and movement rates more precisely in this analysis of Atlantic bluefin tuna.

Estimation of reporting rates in Bayesian frameworks

Reporting rates for conventional tags can be estimated from tagging data, with an assumption regarding model structure: conventional tag reporting rates are lower than archival tag reporting rates, most likely due to the reward differences ($1000 versus a hat). Tag-recapture data can be informative about exploitation rates if recapture and reporting rates are high and the tagging program is properly designed (Martell and Walters 2002; Pine et al. 2003). The common occurrence of nonreporting of recaptured tags, however, produces large uncertainties about *F* estimates. Although tagging data by themselves contain some information on reporting rates, the information is generally weak and the estimates are unstable without auxiliary information in the framework of the maximum likelihood method (Hoenig et al. 1998; Polacheck et al. 2006). Within a Bayesian framework, these uncertainties can be incorporated into estimation models easily. Michielsens et al. (2006) set priors for reporting rates from expert opinions; however, the tagging data in their study did not update the priors for reporting rates. In the current study, instead of specifically setting the prior pdfs of reporting rate, the structural model assumption of higher archival tag reporting rates than conventional was applied, based on expert judgment. In addition, the use of informative priors for *F*s and movement rates from the archival tag model, as well as a tight prior for *M*, facilitates the estimation of conventional tag reporting rates. The significant Bayesian update of conventional tag reporting rates, irrespective of archival tag reporting rates, indicates that tag-recapture data include sufficient information on reporting rates. This is the reason that *F* estimates are relatively robust for different archival tag reporting rate assumptions. In this case, the structural assumption might not be necessary, but such assumptions could play more important roles in situations where data are sparser.

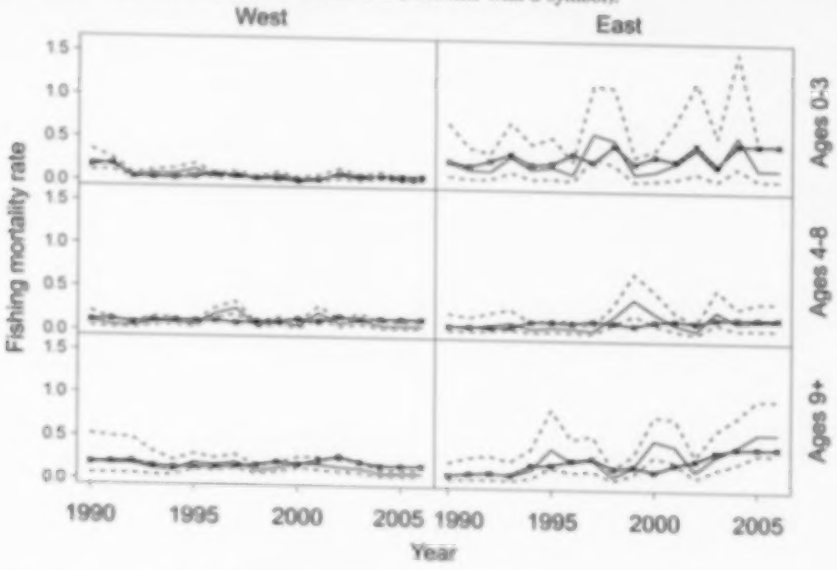
Estimated reporting rates for conventional tags are in the range of 0.06 (after 1999 in the east) to 0.23 (before 1999 in the west) for the base-case scenario. Recent rates after 1999 are half of earlier rates before 1999, and eastern rates are half of western rates. The reason for the apparent drop in reporting rates is hard to pinpoint and may be due to fluctuation in the number of releases over a given set of years prior to the recapture year and changes in fishing operations such as increased tuna penning in the Mediterranean Sea. A change in stock composition would also be plausible as a cause for changing return rates. When the tagged fish are predominantly western in origin, their interaction is with American and Canadian fleets. When fish are eastern, the number of fleets for potential recapture increases to greater than 10 and reporting rates may be lower due to lower transfer of educational information about the tag-recapture programs to some of these fleets.

Conventional tag reporting rates of longline fleets for southern bluefin tuna were estimated from observer data and port sampling in the 1990s. They ranged from 20% to 60%, though variance was relatively large (Eveson and Polacheck 2005; P. Eveson, CSIRO Marine and Atmospheric Research, Castray Esplanade, Hobart, Tasmania 7001, Australia, personal communication, 2006). Australian observers visited almost all Japanese vessels entering Australian ports to collect conventional tags in the 1990s, which supports the notion that conventional tag reporting rates here may be higher than those in Atlantic bluefin tuna fisheries. Hearn et al. (1999) point out that reporting rates might vary over years and ages. In this case, observer data would be helpful to estimate reporting rates more precisely, though they were not available for the present analyses.

Stock status, migration, and stock structure of Atlantic bluefin tuna

In general, the *F* estimates of this study overlapped the ICCAT's *F*s, which are estimated by a VPA model that

Fig. 6. Comparisons between results for the base-case scenario (solid line, posterior median; broken lines, 10th and 90th percentiles of the posterior) and ICCAT (2007) *F* estimates for Atlantic bluefin tuna (bold line with a symbol).



does not use tagging data (Fig. 6; ICCAT 2007). ICCAT's estimates of *F* are used as priors of the present analysis, which may in part explain the similarity, particularly in the east where the tag data were limited. The *F* estimates in the west, however, result from Bayesian updating with tagging data and the priors have little impact. This might indicate that tagging data have information regarding the exploitation rate consistent with the catch-at-age data and stock abundance indices used for the ICCAT stock assessment. It is interesting that the electronic tagging data, which are based mostly on deployments at a few isolated locations, should yield information so similar to the catch-at-age and stock abundance indices, which are based on fisheries that are spatially much more dispersed.

The similarity between the tagging-based estimates of *F* and ICCAT stock assessment results lend support to ICCAT's recent cautions that the current *F* levels for Atlantic bluefin tuna may not be sustainable in both areas (ICCAT 2007). The high *F* estimates for large fish (ages 4–8 and 9+) in the west since the 1990s, which are similar to the assumed natural mortality rate, indicate that fisheries might have considerably impacted fish population dynamics and reduced its resilience. Furthermore, *F* levels in the east have been higher than in the west and most likely increasing in the last decade. It might be necessary to reduce fishing effort quickly to return harvests to sustainable levels. It is, however, noted that the recent estimates of *F* in the west, especially for ages 9+ since 2002, were lower compared with ICCAT's results and the natural mortality estimate, although the difference is unlikely to be significant. These low estimates might be associated with changes in reporting rates and (or) movement rates and possible lags in the reporting and compilation of the most recently recaptured tags.

The current study analyzes extended versions of the tagging data sets evaluated in Block et al. (2005). The current study, however, attempts to reduce possible biases in movement rate estimates that may be caused by *F* differences between areas. We obtained higher estimates of movement rates from west to east than those reported by NRC (1994) (about 1%), which was based on conventional tagging data before the 1990s (Mather et al. 1995). As Block et al. (2005) point out, this potentially is associated with large fish being tagged and consistent with a two-component model for west-to-east movements with adolescent eastern-origin fish tagged in the western Atlantic returning to natal spawning grounds and large western fish moving into the central and eastern Atlantic foraging grounds. The higher estimates of movement rates in the current study might indicate that the proportion of eastern fish in the western fishery has increased over this period. Such changes in stock composition in the west could also explain the low return rates of conventional tags after the 1990s. It could be that before 1990, it was mostly western fish being tagged and western recoveries of residential fish, whereas after this period, the fraction of eastern fish in the west increased, and hence, the tagging of them has increased, as well as apparent dispersal to the east as a consequence. Consistent with this hypothesis is the observation by Block et al. (2001, 2005) that western fish tend to remain, for a significant portion of adolescent years, in the western management unit. Thus, if conventional tags were deployed on primarily adolescent western fish, results from the electronic tagging imply that they would remain primarily in the western management unit and thus would be more recoverable by local fishers. Sibert et al. (2006) also suggest that influences of oceanographic conditions in a given year might have an influence on migration patterns. These considerations suggest that one improvement of the model would be to account for stock structure, including stock origin (e.g., genetics or otoliths), stock mixing, and stock-specific movement patterns with season and environmental information.

Limitation of the current models and future research

In addition to ignoring stock structure, the current study relies on several simplifying assumptions. In some cases, the fraction of Bayesian p values falling between 2.5% and 97.5% was relatively small, e.g., 27% and 43% in the case that the number of observed tag returns was more than 1 and 2 (n = 265 and 92), respectively, with many values falling below 2.5%. This indicates that overdispersion occurs in the data relative to that presumed in the probability model for the data, i.e., observed variances are larger than those expected from the Poisson distribution (Hilborn and Mangel 1997). This might result from the violation of the Poisson assumptions of random sampling and complete mixing of tagged and untagged fish, which is caused by several factors such as highly selective fishing behaviors and high degree of school fidelity of fish. Moreover, the application of a negative binomial model, in which the variance can be larger than the mean, did not improve greatly the model prediction except for the pop-up tag model (the faction of Bayesian p values between 2.5% and 97.5% was 31% and 50% for the conventional tag model when the number of observed tag returns was more than 1 and 2, respectively). This overdispersion might be related to many "zero" return data due to the small number of tag releases and low recapture and reporting rates. In fact, almost 90% of the observed return data for each release and recapture year, age, and area was represented by zero counts. Though statistical modeling considering such overdispersion might become more complicated, zero-inflated and hurdle models may be more appropriate to analyze such zero-inflated data (Cunningham and Lindenmayer 2005; Martin et al. 2005). The overdispersion issue might lead to underestimation of parameter variances and suggests that caution be taken in the interpretation of uncertainties.

Movement rate estimates largely depend on pop-up satellite tag data. However, it is plausible that movement rates from pop-up tagged fish may be low due to the short duration of these tags and season in which these tags are installed. The present model also assumes that fish move from west to east, or vice versa, only once a year. If fish cross over frequently within a year, annual migration rates from this model are likely to be underestimated. Although evidence indicates that multiple crossings by individuals in a single year does occur, our preliminary analysis showed that return crossover rates within a year are relatively low. However, this is dependent on the length of a data record and the type of tag deployed. Short tag deployments (e.g., pop-up satellite tags) by their nature will not have the time to show multiple crossings. The analysis also assumes one aggregated fishery in each area and does not consider differences among fleets in Fs and reporting rates. In contrast, Carruthers (2007) analyzed conventional tagging data for Atlantic swordfish using a more complicated Bayesian model and estimated exploitation rates by fleets. In addition, this model adopted the two-area model based on the ICCAT geographical delimitation. We realize, however, that in the future, finer-scale zoning will be more appropriate if proper area definitions can be determined. To estimate the migration pattern in a detailed spatiotemporal scale based on proper zoning, it will be necessary to utilize track information of pop-up and archival tags between the release and recapture points and develop a more detailed model, considering seasonal movements and including a variety of fishery-related data. Tags released from the eastern management unit also could improve parameter estimates such as east-to-west movements and Fs in the east.

Despite some limitations in the model, this study provides the first comprehensive framework to combine multiple data sources from tagging experiments to estimate exploitation and movement rates. This methodology could be applied widely to other fish populations and species. In addition to electronic tagging, genetic and otolith microchemistry analyses have been applied to Atlantic bluefin tuna to validate and quantify the extent of mixing between the putative stocks with more precision than is currently possible. Integration of such information is essential to the understanding of temporal and spatial population dynamics of each spawning stock, their seasonal overlap, and timing of separation. Together these methods offer significant improvements in resolving long-standing issues in the fisheries management of bluefin tuna (Block et al. 2005; Fromentin and Powers 2005).

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Appendix A

Summary results for the base case of the pop-up satellite tag model and the archival tag model are provided in Tables A1 and A2 and Fig. A1, which follow.

Fig. A1. Posterior distribution of fishing mortality rates of each age group and area from the archival tag modeling. Solid line represents the posterior median. Broken lines represent the 10th and 90th percentiles of the posterior. The dotted line represents the posterior median of the natural mortality rate.

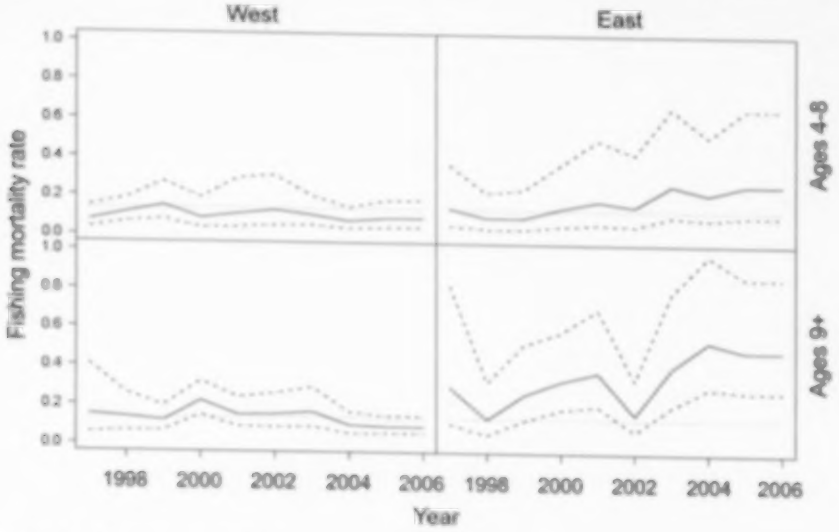

Table A1. Summary results for the pop-up satellite tag model.

Parameter	Age	Area	Scenario 1 (base case) Mean (SD)	Scenario 14 Mean (SD)
Movement rate				
$T_{2,1,2}$	4–8	West to east	0.096 (0.037)	0.107 (0.044)
$T_{3,1,2}$	9+	West to east	0.113 (0.043)	0.114 (0.046)
$T_{2,2,1}$	4–8	East to west	0.210 (0.170)	0.227 (0.188)
$T_{3,2,1}$	9+	East to west	0.631 (0.235)	0.631 (0.239)
Not shed or malfunction				
W			0.888 (0.029)	0.866 (0.037)
Pop-off probability prior				
B			1.377 (0.261)	1.381 (0.262)
Pop-off probability				
$O_{1,1}$			0.965 (0.020)	0.962 (0.025)
$O_{1,2}$			0.035 (0.020)	0.038 (0.025)
$O_{2,1}$			0.175 (0.053)	0.175 (0.064)
$O_{2,2}$			0.793 (0.055)	0.790 (0.066)
$O_{2,5}$			0.032 (0.021)	0.035 (0.024)
$O_{3,1}$			0.221 (0.040)	0.222 (0.053)
$O_{3,2}$			0.397 (0.047)	0.324 (0.061)
$O_{3,3}$			0.358 (0.048)	0.427 (0.066)
$O_{3,4}$			0.024 (0.014)	0.028 (0.018)
$O_{4,1}$			0.272 (0.054)	0.257 (0.063)
$O_{4,2}$			0.333 (0.057)	0.330 (0.067)
$O_{4,3}$			0.353 (0.059)	0.366 (0.071)
$O_{4,4}$			0.021 (0.015)	0.023 (0.018)
$O_{4,5}$			0.021 (0.016)	0.024 (0.019)
Overdispersion				
k				4.197 (1.735)

Note: DIC, deviance information criterion; number of parameters (n) represents all except process errors. For scenario 1 (base case), DIC = 425.4 and n = 20; for scenario 14, DIC = 406.7, n = 21.

Table A2. Summary results for the archival tag model (mean values of parameter estimates).

			Scenario												
	Age	Area	1	2	3	4	5	6	7	8	9	11	12	13	14
DIC			365.2	387.2	365.0	372.3	375.8	363.9	366.4	366.4	376.9	364.1	363.8	334.3	367.8
n			45	45	45	45	45	44	47	47	45	46	45	43	46
Parameter															
Average fishing mortality (t: 1997–2006)															
$F_{2,1}$	4–8	West	0.117 (0.029)	0.143	0.108	0.118	0.146	0.117	0.115	0.120	0.272	0.120	0.115	0.122	0.122
$F_{3,1}$	9+	West	0.151 (0.030)	0.227	0.131	0.157	0.224	0.152	0.149	0.150	0.222	0.156	0.143	0.156	0.158
$F_{2,2}$	4–8	East	0.239 (0.079)	0.259	0.233	0.253	0.244	0.238	0.242	0.232	0.816	0.241	0.238	0.231	0.237
$F_{3,2}$	9+	East	0.403 (0.110)	0.567	0.366	0.522	0.440	0.399	0.418	0.388	0.925	0.407	0.387	0.389	0.410
Reporting rate															
$R_{2,1\,1997\text{–}2005}$		West	0.70	0.30	0.90	0.70	0.30	0.70	0.74	0.70	0.70	0.70	0.70	0.70	0.70
$R_{2,1\,2006}$		West	0.36 (0.165)	0.24	0.41	0.30	0.27	0.30	0.35	0.70	0.33	0.36	0.34		0.36
$R_{2,2\,1997\text{–}2005}$		East	0.70	0.30	0.90	0.30	0.70	0.70	0.62	0.70	0.70	0.70	0.70	0.70	0.70
$R_{2,2\,2006}$		East	0.25 (0.120)	0.17	0.29	0.19	0.20	0.30	0.24	0.70	0.23	0.25	0.23		0.24
Movement rate															
$T_{2,1,2}$	4–8	West to east	0.090 (0.031)	0.098	0.085	0.115	0.080	0.090	0.095	0.089	0.068	0.092	0.090	0.092	0.098
$T_{3,1,2}$	9+	West to east	0.162 (0.038)	0.187	0.152	0.205	0.149	0.160	0.170	0.158	0.135	0.162	0.158	0.157	0.166
$T_{2,2,1}$	4–8	East to west	0.204 (0.166)	0.197	0.211	0.177	0.218	0.204	0.200	0.206	0.234	0.201	0.206	0.205	0.219
$T_{3,2,1}$	9+	East to west	0.373 (0.201)	0.320	0.404	0.259	0.424	0.374	0.350	0.385	0.563	0.367	0.399	0.408	0.373
Degree of mixing															
Ffy_1		West	0.392 (0.151)	0.562	0.339	0.384	0.576	0.389	0.382	0.380	0.230	0.388	0.402	0.378	0.386
Ffy_2		East	0.247 (0.189)	0.344	0.220	0.338	0.251	0.246	0.260	0.253	0.141	0.243	0.252	0.242	0.243
Natural mortality															
M			0.136 (0.013)	0.121	0.140	0.129	0.126	0.135	0.135	0.137	0.137		0.088	0.135	0.136
M_2												0.201			
M_3												0.110			
Overdispersion															
k															6.472

Note: Standard deviations (SDs) for scenario 1 (base case) are given in parentheses after the mean. All other SDs are given in the supplementary material (available online from NRC Data Depository). DIC, deviance information criterion; number of parameters (n) represents all except process errors.

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Biogenic calcite–phosphorus precipitation as a negative feedback to lake eutrophication

Stephen K. Hamilton, Denise A. Bruesewitz, Geoffrey P. Horst, David B. Weed, and Orlando Sarnelle

Abstract: Lakes in carbonate-rich watersheds commonly precipitate calcium carbonate as calcite, and this is accelerated by photosynthetic uptake of carbon dioxide. Co-precipitation of phosphate with calcite is one reason that algal growth in such lakes tends to be strongly phosphorus (P) limited. The extent to which calcite precipitation can be a sink for added P, and thus act as a potential negative feedback to eutrophication, was demonstrated using large enclosures within a Michigan lake. Nitrogen and P were added over 45 days in the summer to produce mesotrophic and eutrophic conditions. Algal biomass and production increased markedly with the nutrient additions, elevating the pH (9–10) and greatly increasing calcite precipitation, reducing concentrations of calcium and alkalinity by up to 60%. Sediment traps indicated that calcite sedimentation was a major sink for added P. By the end of the experiment, only about half of the added P remained in the water column. Major ion concentrations in a larger set of Michigan lakes showed calcite precipitation to be widespread, reflecting the abundant carbonate minerals in this glacial region.

Résumé : Dans les lacs situés dans des bassins versants riches en carbonates, il se fait ordinairement une précipitation de carbonate de calcium sous forme de calcite, un phénomène accéléré par l'incorporation de dioxyde de carbone par la photosynthèse. La précipitation de phosphate conjointe à celle de la calcite est une raison qui explique pourquoi la croissance des algues dans de tels lacs a tendance à être fortement limitée par le phosphore (P). Nous avons démontré l'importance de la précipitation de calcite comme piège pour le P ajouté, et ainsi comme rétroaction négative potentielle à l'eutrophisation, à l'aide de grands enclos érigés dans un lac du Michigan. Nous avons fait des additions de N et de P sur une période de 45 jours en été pour produire des conditions de mésotrophie et d'eutrophie. La biomasse et la production d'algues ont augmenté de façon marquée après l'addition des nutriments, ce qui a fait monter le pH (9–10) et a accru fortement la précipitation de calcite, réduisant ainsi les concentrations de calcium et l'alcalinité de jusqu'à 60 %. Des trappes à sédiments montrent que la sédimentation de calcite sert d'important piège pour le P ajouté. À la fin de l'expérience, il ne demeurait qu'à peu près la moitié du P ajouté dans la colonne d'eau. Les concentrations d'ions majeurs dans un ensemble plus étendu de lacs du Michigan indiquent que la précipitation de calcite est répandue, ce qui est un reflet de l'abondance des minéraux carbonatés dans cette région glaciaire.

[Traduit par la Rédaction]

Introduction

Groundwater-fed lakes in regions where carbonate minerals occur in the rocks and soils are rich in dissolved Ca^{2+} and HCO_3^- and commonly precipitate calcium carbonate in the mineral form of calcite ($CaCO_3$). Such lakes are particularly common in glaciated regions of North America and Europe. In temperate climates, calcite precipitation increases greatly during the summer as a result of both seasonal warming, which reduces the solubility of calcite, and enhanced photosynthetic uptake of carbon dioxide (CO_2) by algae and vascular plants (Kelts and Hsü 1978). Algal and plant growth in such lakes tends to be strongly limited by phosphorus (P) availability (Wetzel 2001), and above pH ~9, the co-precipitation of phosphate with calcite contributes to the limited availability of P. The precipitation of calcite, its binding with P, and its rapid sedimentation out of the water column present a potential negative feedback to aquatic primary production, potentially ameliorating eutrophication caused by nutrient loading (Koschel et al. 1983; Robertson et al. 2007). In addition to P binding, calcite precipitation can act as a negative feedback to aquatic primary production by attenuation of light in the water column and by flocculation and consequent sedimentation of algal cells (Koschel et al. 1983). Calcite precipitation and deposition on underwater surfaces impact the ecology and biogeochem-

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istry of lakes in many other ways, for example, by binding trace metals and dissolved organic matter and by smothering biofilms and underwater plant leaves, and over time, the accumulation of carbonate-rich lake sediments contributes to the infilling of lake basins (Kelts and Hsü 1978; Wetzel 2001).

Limnological studies of calcite precipitation have been mostly observational in nature, although lab experiments have explored the chemistry of calcite and phosphate co-precipitation (House et al. 1986) and the role of algae in inducing the reaction (Hartley et al. 1995; Olsen et al. 2006). Calcium has been experimentally added to lake water in enclosures to abiotically increase calcite supersaturation and strip out P via co-precipitation (e.g., Dittrich et al. 1997). Here we report results from a large-scale enclosure experiment in an oligotrophic lake in Michigan (USA). We sought to determine how nutrient additions affect calcite precipitation and co-precipitation of phosphate via stimulation of algal growth, thereby creating a sink for added P and potentially attenuating the eutrophication response to P loading. We monitored calcite precipitation and concomitant removal of P in large enclosures (~37 000 L) to which we periodically added nitrogen (N) and P over 45 days in the summer to produce mesotrophic and eutrophic conditions. This experiment demonstrates how nutrient loading, via stimulation of phytoplankton growth, draws down dissolved CO_2 and elicits biogenic calcite precipitation, with consequent loss of dissolved Ca^{2+}, carbonate alkalinity, and P from the water column. Comparison of these results with data from lakes across southern Michigan shows that calcite precipitation is widespread and is likely to be important as a negative feedback to eutrophication.

Materials and methods

The enclosure experiments were conducted in Gull Lake (surface area = 8.2 km^2, mean depth = 12 m, maximum depth = 31 m), an alkaline, groundwater-fed lake in southwestern Michigan. Gull Lake is low in P (summer total P in the epilimnion is ~5–12 $\mu g \cdot L^{-1}$) and oligotrophic to mesotrophic in productivity. A water budget for the lake indicated that groundwater supplies 75% of the annual input, either directly via underwater seepage (40% of annual input) or indirectly via spring-fed streams (Tague 1977). Calcite precipitation is readily visible on underwater surfaces during the summer, and the sediments are rich in calcite.

Large tubular enclosures (diameter, 2.5 m; depth, ~8 m; volume, ~37 000 L) constructed of clear polyethylene were suspended from a floating platform at a 15 m deep nearshore site in Gull Lake. Enclosures were open to the atmosphere at the top and sealed from the sediments at the bottom and extended through the ~8 m deep epilimnion but not into the metalimnion (the thermocline in the lake was at a depth of ~10 m). Enclosures were installed and filled with lake water during the first week of July 2005, with nutrient additions performed weekly beginning on 9 July (day 1).

The nine enclosures were randomly assigned to three treatments: control (no nutrients added), medium nutrient availability (target total P = 20 $\mu g \cdot L^{-1}$), and high nutrient availability (target total P = 40 $\mu g \cdot L^{-1}$). P and N were added as a concentrated solution of reagent-grade inorganic P (as $NaH_2PO_4 \cdot H_2O$) and N (as $NaNO_3$) with a molar N–P ratio of 20. The nutrient solution was added through a tube that was slowly raised through the water column. Each week, the required volume of concentrated nutrient solution was determined for each enclosure based on its target total P concentration and the actual concentration measured 2 days prior to the addition.

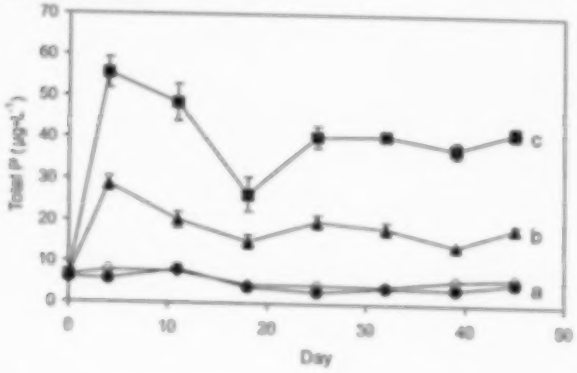
Water samples were collected with a vertically integrating tube sampler from the enclosures, as well as from the lake beside the platform on days 0 (8 July, just before adding nutrients), 4, 11, 18, 25, 32, 39, and 45 (22 August), spanning a period of stable summer stratification of the lake water column. Sampling was performed 4–6 days after each weekly nutrient addition. Temperature, dissolved oxygen, and pH at depths of 0.5 and 6 m were measured during midday with a Hydrolab multisonde. Measurements were made in random order over ~90 min, and the data from the two depths were averaged for comparison with integrated water samples. The pH electrode was calibrated with buffers of pH 7.0 and 10.0. Water samples were immediately taken to a lakeside laboratory in completely full carboys. Vacuum filtration was performed within 1–2 h after water sampling, and labile nutrients, major ions, and chlorophyll *a* concentrations were analyzed within 24 h.

Solutes were measured in water filtered using Gelman (now sold as Pall) A/E glass-fiber filters. Concentrations of major cations (Ca^{2+}, Mg^{2+}, Na^+, K^+) were measured by flame atomic absorption spectrophotometry, adding 0.5% HNO_3 as a preservative. An acidic solution of lanthanum was added before measurement of Ca^{2+} and Mg^{2+} to suppress interferences. Concentrations of major anions (Cl^-, NO_3^-, and SO_4^{2-}) were measured by Dionex membrane-suppression ion chromatography. Total alkalinity was determined by Gran titration with HCl over a pH range of 4.0 to 3.3 (Cantrell et al. 1990). Soluble reactive P (SRP) and ammonium (NH_4^+) were analyzed using standard colorimetric techniques and long-pathlength spectrophotometry (Wetzel and Likens 2000). Total P was analyzed via persulfate digestion followed by colorimetric analysis of SRP. The calcite saturation index was calculated from major ion concentrations, pH, and temperature (Kempe 1982). The saturation index is the $\log_{10}$-transformed ratio of the ion activity product (IAP) to the calcite solubility product (K_{sp}); values above zero imply theoretical supersaturation.

Particulate matter in the integrated water samples (seston) was collected on glass-fiber filters (Gelman A/E, 1.0 μm effective pore size) and immediately frozen. Chlorophyll *a* was extracted from the filters in cold 90% ethanol and measured via fluorometry (Welschmeyer 1994). Acid-soluble Ca and SRP were measured by HCl titration of the particulate matter to pH 3.9, aided by the use of bromcresol green as a pH indicator, adding more acid as needed to maintain this pH for 30 min. At this pH, calcite dissolves while leaving algal cells intact (Vanderploeg et al. 1987). Tests with samples from nutrient-saturated algal cultures indicated that this method produced no detectable leaching of Ca but did leach some P from algal biomass, with no consistent difference between refrigerated and frozen samples (data not shown).

Sedimented material was collected in traps deployed near

Fig. 1. Total P concentrations in the enclosure treatments, including control (●), medium nutrients (▲), and high nutrients (■), and in the lake epilimnion (◇). Letters indicate significant differences ($P < 0.05$). Error bars on this and subsequent figures are standard errors of the mean.



the bottom of each enclosure at day 0, with one set sampled after 12 days and another after 26 days. The traps were plastic cups 6 cm in diameter and 8 cm deep and were deployed to collect sedimented material for chemical analysis rather than to estimate enclosure sedimentation rates. Particulate matter in the traps was suspended in a slurry and collected on filters that were frozen for later measurement of chlorophyll *a* and acid-soluble Ca and P, using the same methods as detailed above for seston samples. Upon removal of the experiment, visual observations indicated that the mass of sedimented organic material and calcite in the bottoms of the enclosures was vastly greater than that of attached algae and calcite on the walls of the enclosures.

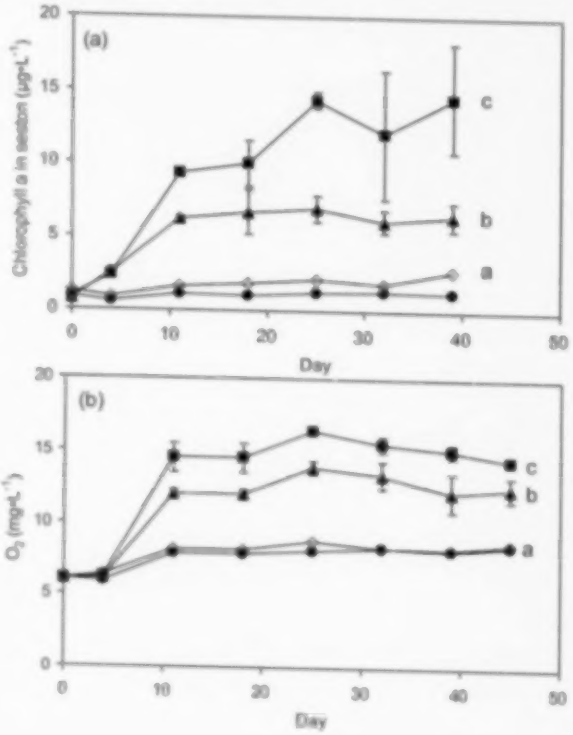
Differences among treatments over time were determined using repeated-measures analysis of variance (ANOVA), and treatment differences in the chemical composition of seston and sedimented material were assessed using one-way ANOVA. Error bars in figures are standard errors of the mean.

Lake surveys were conducted in August of 1998, 1999, 2002, and 2003 from across the Lower Peninsula of Michigan (Raikow et al. 2004; Knoll et al. 2008), and survey data are presented here to compare the degree of calcite precipitation in lakes with what we observed in the experiment. The data in this paper are dissolved Ca^{2+} and Mg^{2+} concentrations in the epilimnion from 141 lake samples, of which 51 samples represent replicate samplings of sites in different years. Sampling and analytical methods were identical to those used in the Gull Lake experiment. These lakes lie on glacial terrain in rural or residential areas, with little potential pollution that would affect their Ca^{2+} and Mg^{2+} concentrations, but with variable degrees of anthropogenic N and P loading from non-point sources such as agriculture and lawn fertilization.

Results

Total P concentrations in the enclosures indicate that after an initial overshoot caused by inaccurate enclosure volume estimates, our target concentrations were approximated with clear differences among the three treatments throughout the

Fig. 2. (*a*) Chlorophyll *a* concentrations and (*b*) dissolved O_2 saturation in the enclosure treatments, including control (●), medium nutrients (▲), and high nutrients (■), and in the lake epilimnion (◇). Letters indicate significant differences ($P < 0.05$ after $\log_{10}$ transformation).

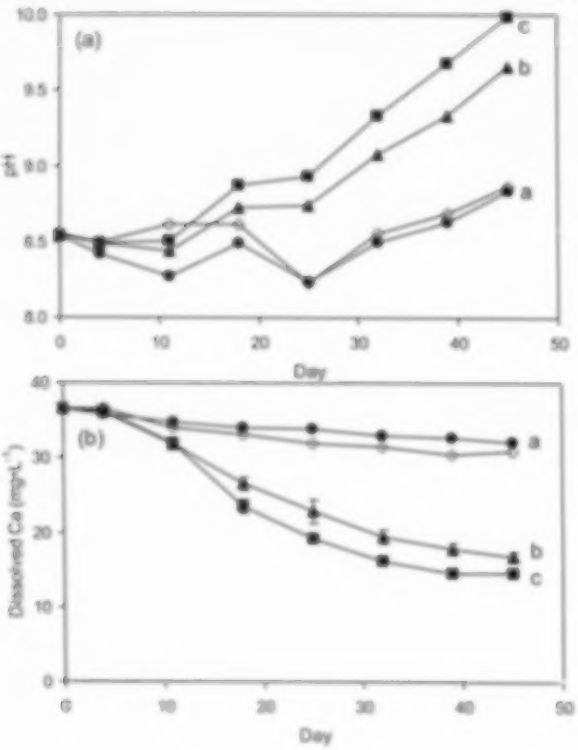


experiment and close correspondence between controls and the lake (Fig. 1). Phytoplankton responded strongly to the P and N additions, increasing in biomass and productivity as reflected by concentrations of chlorophyll *a* (Fig. 2*a*) and dissolved O_2 (Fig. 2*b*). Temperature, dissolved oxygen, and conductance measurements showed that the enclosures remained well mixed throughout the experiment (data not shown).

A marked increase in pH coincided with the increase in phytoplanktonic productivity produced by nutrient additions, reflecting assimilation of dissolved CO_2, and dissolved Ca^{2+} concentrations decreased by up to 60% as pH increased (Fig. 3). Decreases in total alkalinity mirrored those of Ca^{2+}, as expected for precipitation of calcite (Table 1). The other major ions did not change except for a slight increase in Na^+ from the added nutrient salts. Nitrate remained between 0.3 and 0.4 mg N·L^{-1} in the controls but varied more in treatments with added nutrients, and much of the added nitrate was clearly removed (data not shown). Nitrate assimilation by the phytoplankton would have contributed to the elevation of pH, together with CO_2 assimilation (Murphy et al. 1983). Water temperatures ranged from 24.6 to 27.2 °C in the enclosures.

The decrease in dissolved Ca^{2+} was due to calcite precipitation and sedimentation. The calcite saturation index (SI)

Fig. 3. (*a*) pH and (*b*) dissolved Ca^{2+} concentration in the enclosure treatments, including control (●), medium nutrients (▲), and high nutrients (■), and in the lake epilimnion (◇). Letters indicate significant differences ($P < 0.05$, after $\log_{10}$ transformation in the case of Ca^{2+}).



indicated consistent supersaturation by approximately an order of magnitude. The lake and control enclosures began with a calcite SI of 0.98 on day 0 (expressed as the ratio of IAP to K_{sp}, $\log_{10}$-transformed), and by day 45, both had increased to 1.17. The calcite saturation index in the medium- and high-nutrient treatments had increased by day 45 to 1.46 and 1.55, respectively. Acid-soluble Ca was found in the seston and in sedimented material (Fig. 4), and microscopic examination confirmed that calcite crystals were abundant in these samples.

Acid solution of the seston and sedimented material also yielded P, with higher concentrations and sedimentation rates of acid-soluble P in the nutrient-amended treatments compared with the control (Fig. 5). The Ca–P ratios were much lower in the seston than in the sedimented material (Table 2), suggesting selective remobilization of the calcite-bound P as the material sedimented and resided in the traps. Preferential dissolution of P relative to Ca has been observed in calcite sedimenting into a lake hypolimnion (Murphy et al. 1983).

Comparison of acid-soluble P with total P in samples of sedimented material shows that about half of the total P sedimentation losses can be explained by P co-precipitation with calcite (Fig. 6), with the caveats that (*i*) an unknown but probably small fraction of the acid-soluble P could have

Table 1. Concentrations of Ca^{2+} and total alkalinity in the lake and enclosures (means with standard errors in parentheses) at the end of the experiment (day 45).

Treatment	Ca^{2+} ($mg \cdot L^{-1}$)	Alkalinity ($\mu equiv. \cdot L^{-1}$)	pH
Lake	30.9	2.971	8.87
Control	32.1 (0.4)	3.101 (0.011)	8.83 (0.02)
Medium	16.8 (0.5)	2.319 (0.057)	9.66 (0.07)
High	14.6 (0.1)	2.191 (0.094)	9.98 (0.01)

Note: Ca^{2+} and alkalinity are strongly correlated ($R = 0.99$), and decreases in the nutrient addition treatments relative to the control are close to the 2:1 molar ratio of Ca^{2+} to HCO_3^- expected for calcite precipitation. Mg^{2+} concentrations were ~22 $mg \cdot L^{-1}$ and showed no evidence of precipitation in any treatment.

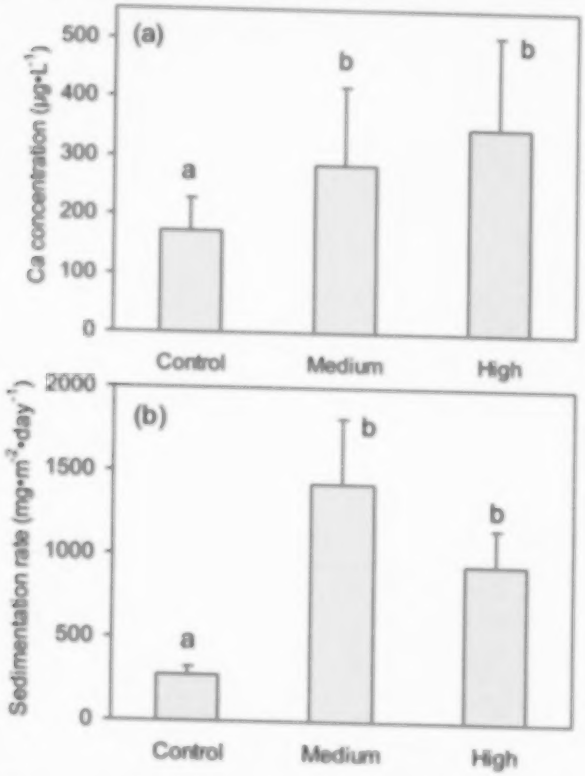
come from algal biomass (Sañudo-Wilhelmy et al. 2004), and (*ii*) some very fine calcite and associated P could have passed through the AE filters, resulting in underestimation of total particulate calcite and acid-soluble P (Dittrich et al. 2004). Iron content in the acid-soluble fraction was below detection limits using flame atomic absorption spectrophotometry, indicating that on a molar basis, there was less iron than P in this material and thus iron-bound P was unlikely to be significant. The remainder of the P that was not soluble in acid was likely to be organic P in living and detrital biomass.

Mass balances of P in the enclosures over the first 26 days were computed in two ways: (*i*) from the decrease in dissolved Ca^{2+} concentration (considered the best indicator of total calcite sedimentation) and the ratio of acid-soluble P to Ca in sedimented material; and (*ii*) from the difference between total P at the beginning and end of the period and the P added over that period. Comparison of these two estimates suggests that sedimentation of P co-precipitated with calcite can explain most to all of the net P loss in the enclosures (Fig. 7).

The total P concentrations measured at the end of the experiment on day 45 can be compared with those that would have been expected in the absence of losses of P from the water column (Fig. 8). The measured total P concentrations averaged 47% of expected concentrations across the medium- and high-nutrient treatments, with no significant difference between the treatments. Thus about half of the P loading evidently sedimented out of the water column, with no evidence of saturation of P sinks at higher P loading rates.

Lake surveys performed during the same season as the experiment show that calcite precipitation is common, as indicated by the departure of lake waters from the groundwater Mg–Ca ratio (Fig. 9). Southern Michigan groundwaters tend to be at equilibrium with dolomite ($CaMg(CO_3)_2$) and calcite in the glacial drift, and thus they have a characteristic Mg–Ca ratio and, in general, are little affected by other sources of these solutes (Hamilton et al. 2007). The median Mg–Ca mass ratio (0.31) is depicted for groundwater in Kalamazoo County, Michigan, where Gull Lake is situated (broken line in Fig. 9, 25 $mg \cdot L^{-1}$ Mg^{2+} and 81 $mg \cdot L^{-1}$ Ca^{2+}; Rheaume 1990). As this groundwater emerges into surface waters such as lakes, streams, and wetlands, calcite precipitation removes Ca^{2+} but the Mg^{2+} is essentially conserved in solution (Stauffer 1985, Szramek and Walter 2004). Rain and snow carry negligible concentrations of Ca^{2+} and Mg^{2+}

Fig. 4. (*a*) Acid-soluble Ca concentration in seston throughout the 45-day experiment and (*b*) rates of sedimentation into the traps over the first 26 days of the experiment. Letters indicate significant differences ($P < 0.05$ after $\log_{10}$ transformation).



(Rheaume 1990) and hence dilute the groundwater but do not affect Mg:Ca at the concentrations found in these lakes, nor does evaporative concentration (unless it contributes to calcite supersaturation). Thus the points depart to the left of the broken line in proportion to the total Ca^{2+} precipitation that has occurred since the groundwater discharged to the surface (Fig. 9).

Our experimental imposition of high nutrient loading to the normally oligotrophic epiliminion of Gull Lake pushed calcite precipitation further than was observed in most Michigan lakes (Fig. 9). Note that the water at the start of the experiment (and in the controls) already had lost more than half of the Ca^{2+} concentration that would have been present in the groundwater entering the lake, based on the leftward displacement from the broken line in Fig. 9. Much of this precipitation may have occurred in previous years; the water residence time of the lake is ~3–4 years (Tague 1977).

Discussion

Loss of P by sedimentation with biogenically precipitated calcite appeared to be an important sink for P added to the experimental enclosures and would have contributed to the amelioration of the impacts of P addition on algal growth.

Fig. 5. (*a*) Acid-soluble P concentration in seston throughout the 45-day experiment and (*b*) rates of sedimentation into the traps over the first 26 days of the experiment. Letters indicate significant differences ($P < 0.05$).

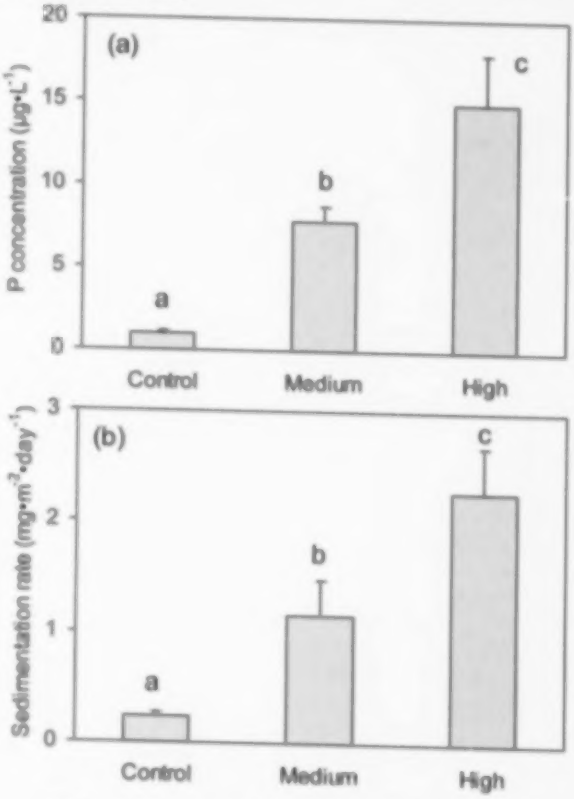


Table 2. Mass ratios of acid-soluble Ca to P in seston (all dates combined) and sedimented material (collected on days 12 and 26).

Treatment	Seston Ca:P	Sedimented Ca:P
Lake	257 (131)	—
Control	198 (67)	2036 (586)
Medium	39 (21)	1113 (615)
High	25 (11)	381 (45)

Note: Data are means with standard errors in parentheses.

This loss mechanism may be particularly important because it removes phosphate, the most bioavailable P form. Both Ca-bound P and organic P are potentially subject to remobilization during sedimentation and in the sediments, and the relative remobilization rates of these P forms in this case are not known. Nevertheless, in a thermally stratified lake, net P loss will occur as sedimenting particles exit the epilimnion, and P that is remobilized below that point does not become available to phytoplankton in the epilimnion until the lake mixes once again (Robertson et al. 2007).

The experimental results reported here are consistent with inferences made in observations of individual lakes in which

Fig. 6. Comparison of acid-soluble P with total P content in sedimented material collected over the first 12 days and the first 26 days (all treatments combined). The broken line is a 1:1 line.

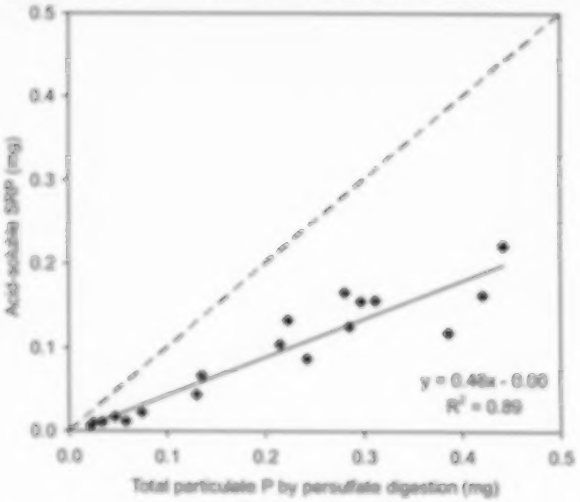


Fig. 7. Enclosure P mass balance for the first 26 days based on the observed drawdown in dissolved Ca^{2+} concentration and the P:Ca in sedimented material (ordinate), compared with the water-column mass balance of total P concentration, with the P additions accounted for (abscissa). Control, ●; medium nutrients, ▲; high nutrients, ■. The broken line is a 1:1 line.

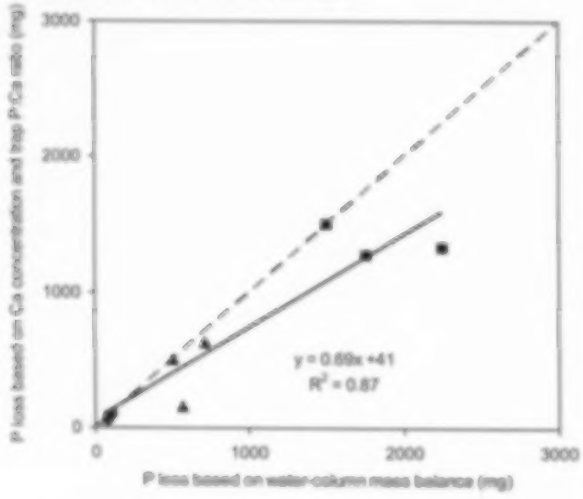


Fig. 8. Enclosure total P concentrations measured at the end of the experiment (day 45) compared with those that would have been produced in the P-addition treatments had no P losses occurred (broken line). The measured total P concentrations averaged 47% of those calculated based on P additions, with no significant difference between medium- and high-nutrient treatments.

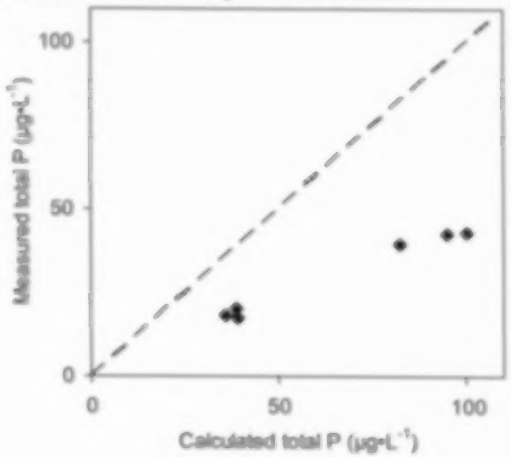
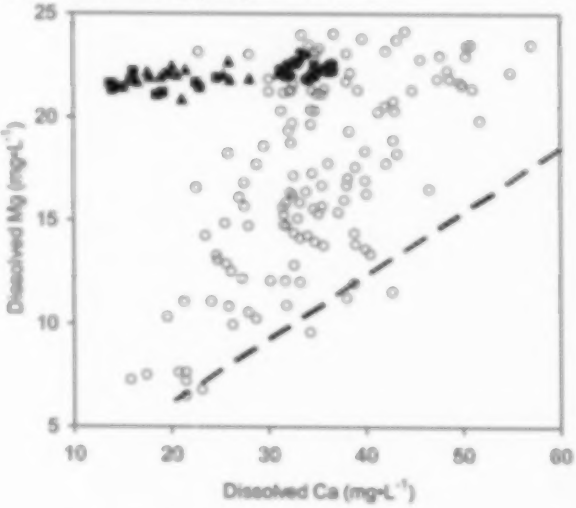


Fig. 9. Comparison of dissolved Mg^{2+} and Ca^{2+} concentrations in lakes across southern Michigan (○) and in the experimental enclosures (control, ●; medium nutrients, ▲; high nutrients, ■). The broken line shows the ratio of dissolved Mg to dissolved Ca in groundwaters; departure of points to the left of the broken line reflects Ca^{2+} removal by precipitation of calcite.



calcite precipitation has been studied. Studies of several lakes have estimated that co-precipitation with calcite could explain 25%–30% of the P removal from the water column, including Lakes Wallersee (Jäger and Röhrs 1990) and Constance (Kleiner 1988) in Germany and the Ca-polluted and eutrophic Onondaga Lake in New York (Effler et al. 1996). In Lawrence Lake, a small, oligotrophic, groundwater-fed lake near Gull Lake, an estimated 61%–76% of P removal was ascribed to calcite co-precipitation (Otsuki and Wetzel 1972). Observed seasonal declines in epilimnetic Ca^{2+} concentrations in individual lakes have ranged from 41% to 48% (Otsuki and Wetzel 1974; Murphy et al. 1983; Stable 1986), less than the 60% decline produced by the high-nutrient treatment in our study but still substantial. The sestonic Ca concentrations that we report here are similar to those measured in Fayetteville Green Lake in New York (Brunskill 1969) and Lake Breiter Lucin in Germany (Koschel et al. 1983). The Ca sedimentation rates shown herein overlap with those reported for Lake Constance

(Stable 1986), Fayatteville Green Lake (Brunskill 1969), and Lawrence Lake (Otsuki and Wetzel 1974) but are higher than were observed in Lake Breiter Lucin (Koschel et al. 1983) and lower than in Onondaga Lake (Effler and Driscoll 1985). We have observed daytime pH values in the range of 9 to 10 in several productive Michigan lakes, and thus the high pH observed in the mesocosms with added nutrients is not unrealistic in the open waters of naturally alkaline lakes with abundant nutrients.

This study provides an experimental demonstration of how calcite precipitation and consequent removal of phosphate are directly coupled to the productivity of phytoplankton and how this process can act as a negative feedback to eutrophication by rapidly removing available P from the epilimnion. These experimental results support the eutrophication feedback hypothesis of Koschel et al. (1983) and are consistent with a number of observational studies of individual lakes cited above. Increased loading of nutrients to lakes that are prone to calcite precipitation will enhance the removal of Ca^{2+} and alkalinity, generating calcite deposits on surfaces and leading to accumulation of calcitic sediments. The massive quantities and reactive nature of calcite deposited in lakes produces myriad ecological and biogeochemical implications. In addition, because calcite is less soluble at higher temperatures, warmer and longer periods of summer stratification associated with climate change would be expected to increase the total seasonal precipitation of calcite, even if rates of primary productivity were to remain unchanged. Where lakes and reservoirs are important hydrologic storages in watersheds, this enhanced calcite precipitation could potentially reduce the flux of Ca^{2+} and alkalinity from land to sea, although at the broader watershed scale, other anthropogenic activities such as agricultural liming may have counteracting impacts (Hamilton et al. 2007).

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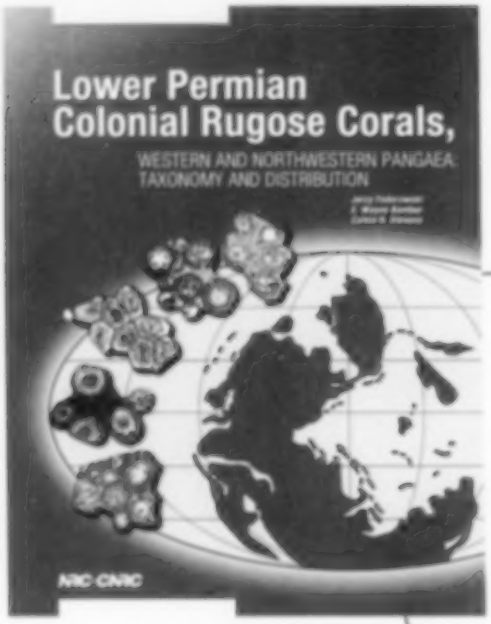

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